Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 40, No. 11, November 1983

Volume 40, n° 11, novembre 1983

Canada

Fisheries and Oceans / Pêches et Océans

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

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Volume 40, No. 11, November 1983

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Nitrogen Fixation and Phosphorus Turnover in a Hypertrophic Prairie Lake[1]

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BROWNLEE, B. G., AND T. P. MURPHY. 1983. Nitrogen fixation and phosphorus turnover in a hypertrophic prairie lake. Can. J. Fish. Aquat. Sci. 40: 1853–1860.

Nitrogen fixation by *Aphanizomenon flos-aquae* in a prairie lake in southwestern Manitoba was dependent on the light intensity and in situ oxygen concentrations. The mean molar ratio of acetylene reduction to nitrogen reduction was 5.8:1. High external ammonium concentrations did not appear to inhibit nitrogen fixation over the short term. Nitrogen fixation was not directly initiated by the bloom collapse. We propose that the coupled sequence of ammonia volatilization and nitrogen fixation was triggered by the bloom collapse and that the bloom collapse was caused by coprecipitation of orthophosphate with carbonates. $^{32}PO_4$ turnover was most rapid during periods when the lake was opalescent, presumably due to carbonate precipitaton.

BROWNLEE, B. G., AND T. P. MURPHY. 1983. Nitrogen fixation and phosphorus turnover in a hypertrophic prairie lake. Can. J. Fish. Aquat. Sci. 40: 1853–1860.

La fixation de l'azote par *Aphanizomenon flos-aquae* dans un lac de prairie du sud-ouest du Manitoba dépend de l'intensité lumineuse et des concentrations d'oxygène *in situ*. Le rapport molaire moyen de la réduction de l'acétylène à celle de l'azote est 5,8:1. De fortes concentrations d'ammonium externe ne semblent pas, à court terme, nuire à la fixation de l'azote. Cette dernière n'est pas directement déclenchée par l'arrêt subit de la floraison. Nous suggérons que la séquence volatilisation de l'ammoniac–fixation de l'azote est déclenchée par l'affaissement de la floraison, cette dernière étant causée par la précipitation de l'orthophosphate en même temps que celle des carbonates. Le renouvellement de $^{32}PO_4$ se produit à un taux maximal durant les périodes où le lac est opalescent, probablement à cause de la précipitation des carbonates.

Received January 7, 1983
Accepted July 5, 1983

Reçu le 7 janvier 1983
Accepté le 5 juillet 1983

[1]This is the third paper in a series on nitrogen metabolism in prairie lakes. The others are Murphy and Brownlee 1981a, 1981b.

Printed in Canada (J7194)
Imprimé au Canada (J7194)

NITROGEN fixation by blue-green algae is an important reaction in lakes because it may be a mechanism by which these algae survive and dominate under low nitrogen conditions. In many productive prairie pothole lakes the ammonia content oscillates from levels toxic to rainbow trout (*Salmo gairdneri*)

to levels low enough to induce very high rates of nitrogen fixation (Barica 1975a). In our study lake, nitrogen fixation by *Aphanizomenon flos-aquae* often followed periods of rapid ammonia volatilization (Murphy and Brownlee 1981a). These nitrogen reactions were preceded by a period of high phosphate demand and carbonate precipitation. This sequence of reactions may be common in the more eutrophic prairie pothole lakes where attempts to raise rainbow trout are often unsuccessful.

Nitrogen fixation is usually measured by the acetylene reduction method because this technique is fast, inexpensive, and sensitive. A major problem with this reaction is that it is an indirect method and the conversion from units of acetylene reduction to nitrogen fixation is not constant. Differences between studies that did calibrate their acetylene reduction assays with ^{15}N may be due to hydrogen production with N_2 as substrate (Peterson and Burris 1976; Graham et al. 1980), or biological utilization of ethylene in the acetylene reduction assay (Flett et al. 1975). Moreover, because physiological studies have used only a few blue-green algal species, there is no assurance that the nitrogen fixation reactions are identical in all blue-green algae. Acetylene may react with the nitrogenase complex quite differently than does nitrogen, and environmental changes in oxygen concentration could affect the acetylene-nitrogenase reaction quite differently than the nitrogen−nitrogenase reaction.

Direct measurements can be made with the stable isotope ^{15}N, using isotope ratio mass spectrometry as the traditional method of analysis. Because the analysis has been difficult, the number of ^{15}N studies of nitrogen fixation in lakes is small. In 1977, we carried out nitrogen fixation experiments in a small, hypertrophic lake to determine the importance of nitrogen fixation in this type of lake, and to calibrate acetylene reduction rates with ^{15}N measurements using optical emission spectrometry as an alternative method of measuring ^{15}N. Optical emission spectrometry is fast, requires small samples, and the equipment is much easier to maintain than most mass spectrometers (Madsen 1979; Flett et al. 1980; Murphy 1980). This optical method does require a relatively high incorporation of ^{15}N (0.2 atom % excess) but this enrichment is easily obtained in the large populations of blue-green algae which often actively fix nitrogen in many lakes of the Canadian prairies.

Study Site

Lake 885 is located in the Erickson−Elphinstone area of southwest Manitoba (50°30′N, 100°10′W). Because of their high productivity, lakes in this area have been the subject of intensive aquaculture studies (Lawler et al. 1974; Ayles et al. 1976). Lake 885 has been studied intensively because it commonly experiences a serious problem observed less frequently in less productive lakes. Dense blooms of *Aphanizomenon flos-aquae* usually form several times during the summer (Barica 1974) and the collapse of these blooms can lead to fish summerkills (Barica 1975b; Papst et al. 1980). In 1977, large enclosures (228 000 L) were placed in this lake by researchers from the Freshwater Institute, Winnipeg. One enclosure (+N) was enriched with ammonium nitrate (0.75−1.5 g $N \cdot m^{-2} \cdot wk^{-1}$; Barica et al. 1980) and the other (+P) was enriched with phosphate (0.05−0.1 $g \cdot m^{-2} \cdot wk^{-1}$; J. Barica, personal communication). Nitrogen fixation was studied in the lake and in these enclosures. Lake 885 has an area of 2.4 ha, maximum depth of 2.9 m and mean depth of 1.9 m (Papst et al. 1980). Algal composition and succession in this lake have been described by Kling (1975).

Methods

Acetylene reduction was measured by a method similar to that of Flett et al. (1976). Water samples of 30 mL were treated with 5.0 mL of acetylene, with exclusion of air, in 50 mL syringes fitted with needles which were pushed into rubber stoppers. This ratio of sample to acetylene was chosen after doing some preliminary experiments with various volumes of acetylene. The syringes were shaken gently to dissolve the acetylene, and then incubated in situ for 1 h using plastic holders which kept the syringes horizontal. Ethylene was extracted by drawing in 15 mL of air to the syringe, stoppering, and shaking vigorously. Blanks were obtained from samples which had been treated with acetylene and extracted immediately without incubation. The vapor phase was transferred to sample vials by displacement of water and analyzed within a few hours by gas chromatography on a Hewlett-Packard 5720 instrument equipped with a flame ionization detector and a 1.8 m by 3 mm column packed with Porapak N. Peak areas were integrated with a Hewlett-Packard 3380 integrator. Ethylene standards were obtained from Alltech Associates (Arlington Heights, IL).

$^{15}N_2$ was prepared by the method of Burris (1976) by hypobromite oxidation of $(^{15}NH_4)_2SO_4$ (Bio-Rad, 95 atom % ^{15}N), and transported to the field in sealed glass syringes.

Water samples (40 mL) were placed in 50-mL glass syringes with all air excluded. The samples were then treated with 10 mL of $^{15}N_2$:O_2 mixture (pO_2 and pN_2 were varied) taking care to avoid atmospheric contamination. Dissolved $^{14}N_2$ was not removed from the samples in order to minimize physical manipulation of the algae. The syringes were shaken gently to equilibrate added and ambient N_2, then incubated in situ. ^{15}N:^{14}N ratios in the N_2 were calculated from the added and ambient amounts assuming an ambient concentration of 0.5 mmol L^{-1} (Stumm and Morgan 1981). Lake water samples (40 mL) were treated with air (10 mL) and incubated in situ to provide blanks for ambient ^{15}N values. After the incubation was complete, dissolved oxygen concentration was measured in the sample with an oxygen probe, and the algae were collected on precombusted (450°C for 3−4 h) Whatman GF/C filters and stored frozen until analysis at NWRI (Burlington, Ontario). Uptake of ^{15}N (nitrogen fixation) was calculated from the atom % excess of ^{15}N and particulate nitrogen values. ^{15}N and particulate nitrogen analyses were done as previously described (Murphy 1980).

Light measurements were made with a LI-COR 85 meter (Lambda Instruments Corp., Lincoln, NE) equipped with underwater quantum sensor. Oxygen and temperature measurements were made with a Yellow Springs Instruments model 54 meter calibrated against air-saturated water.

Phosphate turnover times were determined by the radioisotope method of Lean (1973). Carrier-free $^{32}PO_4$ was added to water samples of about 200 mL collected from 0.5 m.

TABLE 1. Acetylene reduction rates for unconcentrated and concentrated (>70 μm) water samples from Lake 885.

Concentration factor	C_2H_2 reduction nmol·L^{-1}·h^{-1} [a]	Mean (SD)
Whole lake water (×1)	277, 264 252, 276	267 (12)
×10	330, 329 323, 319	325 (5)
×70	177, 178 158, 158	168 (11)

[a]Results of duplicate analysis of duplicate samples.

Subsamples of 5.0 mL were taken by pipet at sufficient frequency to give a good kinetic plot and filtered through a 0.45 μm membrane filter (Sartorius). ^{32}P activity remaining in the filtrate was counted at 47% efficiency as Cerenkov radiation on a Searle Delta 300 liquid scintillation counter. Soluble reactive phosphorus (SRP) was analyzed in the Erickson field laboratory by FWI staff using the acid-molybdate-ascorbic acid method of Murphy and Riley (1962).

The samples used for calcium analysis had been filtered, frozen, and freeze-dried. They were redissolved by shaking for one week in a mixture of 5% HNO_3 and 5% HCl, and analyzed for calcium on a Perkin-Elmer atomic absorption unit with a nitrous oxide/acetylene flame.

Results and Discussion

Acetylene Reduction

The first preliminary experiment was done with 2.0, 4.0, 5.0, and 6.0 mL of acetylene per 30 mL of sample. The optimal rate of acetylene reduction was achieved with 4.0–5.0 mL of acetylene and all further experiments used 5.0 mL of acetylene. A second preliminary experiment was done to determine the effect of concentrating samples on 70 μm Nitex screens, which retained all of the *Aphanizomenon* trichomes. When corrected to the original sample volume, unconcentrated samples were more active than the samples concentrated 70 fold but slightly less active than the 10 fold concentrated samples (Table 1). This illustrates that the algae are sensitive to sample concentration and that the dominant alga, *Aphanizomenon*, was responsible for the nitrogen fixation. The assay was sensitive enough that we chose to do all future experiments with unconcentrated samples.

On June 16 two depth profile experiments were done in the lake. In the first, a series of samples collected at 0.5 m intervals from 0 to 2.5 m were incubated at the depth from which they were collected (Fig. 1a). Strong surface inhibition is evident. The second experiment consisted of incubating a set of samples of 0.5 m water at 0–2.5 m in 0.5-m intervals (Fig. 1b). These algae had similar nitrogen fixation (C_2H_2) rates at depths of 0–1.0 m. Below this the rates decreased, but not as rapidly as in the preceding experiment. These algae were able to tolerate some degree of changing light levels and

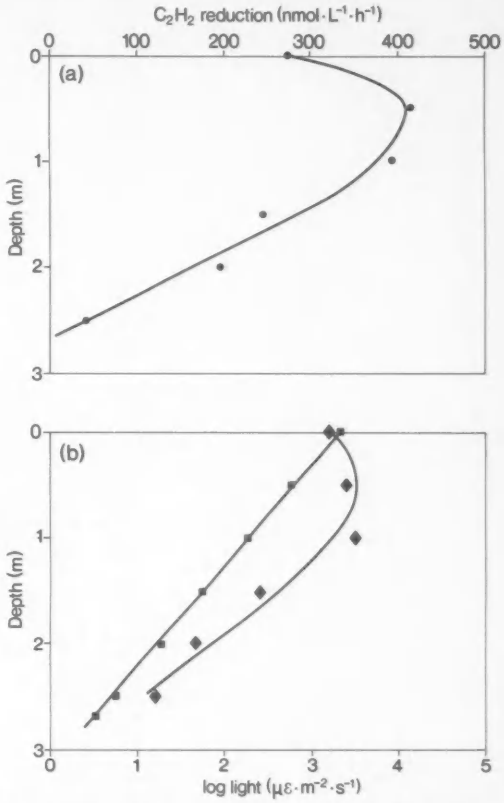

FIG. 1. a, Depth profile for acetylene reduction in Lake 885, June 16, 1977. b, Effect of in situ light level (■) on acetylene reduction (◆) by algae from 0.5 m incubated at different depths in Lake 885, June 16, 1977. Acetylene reduction scale is the same as in Fig. 1a.

still maintain nitrogen-fixing (C_2H_2) activity over short incubation periods. Based on these observations, 0.5 m was chosen as the optimal depth for most of the sampling and incubation. Integration of the depth profile provided a conversion factor of 1.7 to convert 0.5 m volumetric rates to areal (m^{-2}) rates. The depth profile obtained for Lake 885 was very similar to that reported by Flett et al. (1980) for Lake 226 in the Experimental Lakes Area.

Nitrogen fixation (C_2H_2) was measured hourly at 0.5 m in the +P enclosure for most of July 2 from early morning to sundown (Fig. 2). The decrease in nitrogen-fixing (C_2H_2) activity between 13:00 and 18:00 is rather striking. This coincided with the passage of a storm front with high winds and reduced sunlight. The reduced activity may also be a response to high oxygen levels which developed in the enclosure during the day (Ohmari and Hattori 1979; also see the section on ^{15}N experiments). Since this experiment was not repeated, the cause and frequency of this diurnal pattern remain

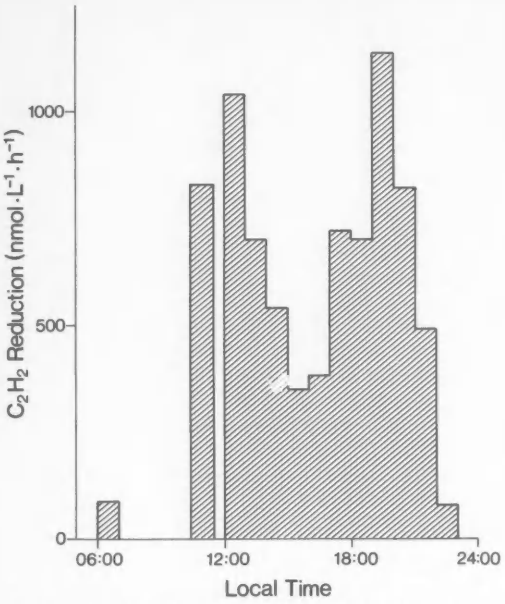

FIG. 2. Diurnal acetylene reduction in the Lake 885 +P enclosure at 0.5 m, July 2, 1977.

undetermined. Integration of this curve gives a factor of about 10 to convert midday hourly rates of nitrogen fixation (C_2H_2) to daily rates. These daily rates should be viewed as best estimates only, because the depth profile and diurnal measurements were each made only once.

^{15}N EXPERIMENTS

Calculation of daily rates of nitrogen fixation from hourly midday rates of acetylene reduction required the above conversion factors and the C_2H_2:N_2 ratio. Frequently, the theoretical ratio of 3:1 (Burns and Hardy 1975) is used. An experimentally determined ratio from concurrent $^{15}N_2$ and C_2H_2 experiments is preferable (Peterson and Burris 1976). The high temporal variability of nitrogen fixation in Lake 885 meant that our "calibration" experiments would have to be done under very similar conditions for $^{15}N_2$- and C_2H_2-treated samples.

The results for ^{15}N experiments carried out under a variety of conditions in the lake and +P enclosure are summarized in Table 2. The experiment of June 30 was done with pure $^{15}N_2$ and long incubation time (12.5 h) in an effort to get a large enrichment. The atom % excess ranged from 1.0 to 2.1%. This high level of incorporation of $^{15}N_2$ provides solid evidence for nitrogen fixation by natural populations of *Aphanizomenon flos-aquae* (and any associated bacteria) because of the nearly unialgal conditions.

The experimental design allowed for altering the ratio of nitrogen and oxygen in the vapor phase. The original intention was to allow a close approximation of the in situ oxygen concentration with minimal disruption of the algae. The in situ oxygen concentration was measured at the time of sampling and a suitable nitrogen:oxygen ratio was chosen. At the end of incubation, the oxygen concentration was measured in situ and in the samples. These values are presented in Table 2. On one occasion (June 28) a wide range of nitrogen:oxygen ratios was used (N_2:O_2 = 0.3:0.7 to 1.0:0). The rate of nitrogen fixation was quite sensitive to this ratio. Consequently all values of atom % excess ^{15}N were correlated against dissolved oxygen concentrations and against pN_2. Both cases gave weak and about equal correlations ($r = -0.39$ for atom % $^{15}N \cdot h^{-1}$ vs. dissolved O_2, and $r = 0.37$ for atom % $^{15}N \cdot h^{-1}$ vs. pN_2). Because of the experimental design it is not possible to distinguish between the two possible explanations: (1) the nitrogenase enzyme of the algae is not saturated at lower partial pressures of nitrogen, or (2) oxygen has an inhibitory effect on the nitrogenase system. The latter is the more likely for two reasons: (1) the shape of the atom % excess ^{15}N vs. pN_2 plot (Fig. 3) has the opposite curvature to that for a saturation curve (Madsen 1979; Jensen and Cox 1983), and (2) oxygen has been shown to inhibit nitrogen fixation in laboratory studies with *Anabaena cylindrica* (Ohmori and Hattori 1979). Furthermore, Coulombe and Robinson (1981) concluded that O_2 toxicity contributed to an *Aphanizomenon* decline in Lake 885 in July, 1979. This adds a further complication to the physiology of nitrogen by natural populations of *Aphanizomenon flos-aquae* and perhaps other nitrogen-fixing blue-green algae.

The results used in determining the C_2H_2:N_2 ratio are summarized in Table 3. Only experiments which had concurrent acetylene reduction determinations for the whole time span of the $^{15}N_2$ incubations were used. This was done by using consecutive C_2H_2 incubations of 1 or 2 h, except for the July 1 experiment where both $^{15}N_2$ and C_2H_2 incubations were for 7 h. Incubation times of several hours were required with $^{15}N_2$ to get sufficient incorporation of isotope to be measurable by optical emission spectrometry. The mean value calculated for the C_2H_2:N_2 ratio from these five experiments is 5.8 ± 1.1. Literature values from five studies carried out on lake populations of blue-green algae are included in Table 3 for comparison. All of these ratios are higher than the frequently used ratio of 3:1 by varying amounts. The reasons for this have been discussed in some detail by Peterson and Burris (1976) and by Graham et al. (1980). Both groups ascribe this higher ratio to hydrogen production. With N_2 as the substrate some of the electron flow is diverted to hydrogen production; with C_2H_2 as the substrate this diversion does not occur. The result is an enhanced rate of acetylene reduction giving a higher than theoretical ratio of C_2H_2:N_2 reduction. This ratio is sensitive to dissolved oxygen concentration (Ohmori and Hattori 1979); acetylene reduction is more sensitive than nitrogen reduction to increasing levels of oxygen. Under the usual conditions of the acetylene reduction assay, hydrogen formation is inhibited (Graham et al. 1980). If hydrogen formation is essential for protecting the nitrogenase from oxygen then the conversion factor between the indirect (C_2H_2) and direct ($^{15}N_2$) methods will be dependent on the oxygen regime. Further, careful experimentation is needed to resolve this matter. Until then, quantitative assays for nitrogen fixation

TABLE 2. Summary of experimental conditions and isotope incorporation for ^{15}N experiments done in Lake 885 (L) and the +P enclosure (P) in 1977.

Date and time	DO in lake/ enclosure[a]	DO in sample	pN_2 in sample	^{15}N atom % excess	^{15}N %·h^{-1} incorporated[b]
June 28 (P)	7.9–8.9	8.0	0.83	0.57, 0.47	0.13 (0.02)
12:00–16:00		8.0	0.83	0.32, 0.25	0.07 (0.01)
		3.0	1.0	0.62, 0.83	0.18 (0.04)
		28[c]	0.30	0.13, 0.12	0.03 (0.002)
June 30 (P)	4.2–5.1	2.6	1.0	1.68	0.13
09:00–21:30		2.7	1.0	2.10, 1.71	0.15 (0.02)
		2.8	1.0	1.01	0.08
		2.5	1.0	1.60, 1.86	0.14 (0.01)
July 1 (P)	7.6–14.2	13.3	0.8	0.51, 0.45	0.07 (0.005)
15:30–22:30					
July 2 (P)	11.5–17.4	15.0	0.75	0.50	0.13
12:00–16:00		14.5	0.75	0.28, 0.42	0.09 (0.025)
July 2 (P)	17.4–>20	14[c]	0.70	0.45	0.075
16:00–22:00		13.8	0.70	0.46	0.08
July 3 (P)	18.4–19.0	7.8	1.0	0.21	0.05
18:00–22:00		6.0	1.0	0.23	0.06
		13.6	0.70	0.14	0.035
		12.7	0.70	0.17	0.04
July 13 (L)	17.8	10.2	0.80	0.99	0.20
16:45–21:45		9.0	0.80	0.44	0.09
		9.3	0.80	0.53	0.11
		9.2	0.80	0.69	0.14
July 14 (L)	14.0–16.4	12.4	0.80	0.64	0.16
12:00–16:00		12.0	0.80	0.72	0.18
July 14 (L)	16.4–17.2	10.7	0.80	0.74	0.12
16:00–22:00		11.4	0.80	0.83	0.14

[a]Dissolved oxygen (mg L^{-1}) at beginning and end of experiment.
[b]Standard deviation for duplicate analysis in parentheses.
[c]Calculated from pO_2 in vapor phase.

using acetylene reduction and the "theoretical" conversion factor of 3:1 should be interpreted with some caution.

Relation of Nitrogen Fixation to the Nitrogen Cycle

Nitrogen fixation appears to play a minor but occasionally important role in the nitrogen cycle of Lake 885. The potential nitrogen influx from fixation is small compared to other nitrogen fluxes in this lake but nitrogen fixation may be important to the algae for brief periods following rapid ammonia volatilization (Murphy and Brownlee 1981a). Nitrogen fixation rates never exceeded the rates of ammonium uptake (Murphy and Brownlee 1981b). Ammonium would seem to be the preferred form of inorganic nitrogen used by the algae. There is little evidence for an inverse relationship between nitrogen fixation and ammonium concentration in the short term, as might be expected according to conventional concepts. In fact, some quite high rates of nitrogen fixation were observed when there was an adequate external supply of fixed nitrogen (Table 4, June 16 and July 12 in the lake, and June 28 and 30 in the +P enclosure).

Relation of Nitrogen Fixation to Lake Productivity

The hourly volumetric rates of acetylene reduction and the converted areal rates of nitrogen fixation are given in Table 4 for the lake and the +P enclosure. The measurements were carried out until mid-August but rates were zero or very small and are not included in Table 4. As expected, nitrogen fixation (C_2H_2) in the +N enclosure was zero or very low on all dates when measurements were made. The major effect of the nitrogen loading was due more to a species shift to *Microcystis aeruginosa* which does not fix nitrogen, than to a direct suppression of nitrogen fixation. The +P enclosure had higher maximum rates of acetylene reduction than the lake (2000 vs. 840 nmol·L^{-1}·h^{-1}) and higher accumulated nitrogen fixation (440 vs. 270 mg N·m^{-2}). Thus, nitrogen fixation could be stimulated by addition of phosphorus and stopped by high additions of nitrogen.

The question of phosphorus and nitrogen deficiency for

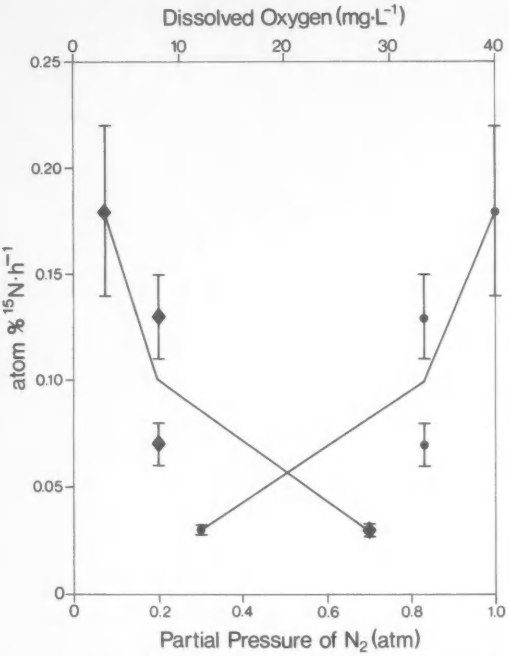

FIG. 3. Uptake of $^{15}N_2$ by algae in the Lake 885 +P enclosure vs. partial pressure of N_2 (●) and dissolved oxygen concentration (◆), June 28, 1977.

TABLE 3. A comparison of C_2H_2:N_2 ratios from this study and the literature.

Date	nmol C_2H_2 mg $N^{-1}\cdot h^{-1}$ (SD)	nmol N mg $N^{-1}\cdot h^{-1}$ (SD)	Ratio C_2H_2:N_2 (SD)
July 1	175	27 (2.4)	6.5 (0.6)
July 2	210 (40)	42 (11)	5.0 (2.3)
July 2	215 (65)	30 (0.5)	7.2 (2.3)
July 14	295 (6)	68 (6)	4.3 (0.4)
July 14	305 (30)	52 (4)	5.9 (1.1)
		mean ratio	5.8 (1.1, n=9)

Literature reference	Range	Mean ratio (SD)
Peterson and Burris (1976)	2.7–6.5	4.4 (0.9, n=12)
Lean et al. (1978)	1.0–11	5.7 (3.5, n=8)
Madsen (1979)	8.4–9.9	9.4 (0.9, n=3)
Flett et al. (1980)	2.1–11.9	7.8 (2.7, n=10)
Graham et al. (1980)	6.7–11.6	8.2 (1.4, n=13)

collapse of *Aphanizomenon* blooms in Lake 885 was studied by Healy and Hendzel (1976). They concluded that the algae were showing signs of phosphorus deficiency and to a lesser degree of nitrogen deficiency prior to bloom collapse. However, neither these nor the other parameters they measured were reliable indicators of an impending bloom collapse.

TABLE 4. Acetylene reduction and nitrogen fixation rates for Lake 885 in 1977.

Date	C_2H_2 reduction nmol·L^{-1}·h^{-1}	mg N fixed $m^{-2}\cdot d^{-1}$	$NH_4^+ - N$ $\mu g\cdot L^{-1}$
		Lake	
June 14	270	22	—
June 16	415	34	330
June 17	460	38	—
June 27	32	2.6	58
June 28	21	1.7	100
June 29	48	3.9	170
June 30	0	0	630
July 1	0	0	660
July 3	22	1.8	590
July 12	840	69	120
July 13	730	60	9
July 14	490	40	17
	Total N fixed	273 mg·m^{-2}	
		+P Enclosure	
June 14	190	16	—
June 17	130	11	—
June 27	740	61	0
June 28	240	20	420
June 29	2000	160	160
June 30	300	25	680
July 1	540	44	—
July 2	1040	85	180
July 3	190	16	30
	Total N fixed	438 mg·m^{-2}	

Nitrogen fixation does not appear to have a causative relationship with bloom collapse either.

RELATION OF NITROGEN FIXATION TO PHOSPHATE AVAILABILITY

The $^{32}PO_4$ turnover times and SRP analyses for the lake and the two enclosures are given in Table 5. Low SRP values are not a reliable indicator of high phosphorus demand, but the results are included to show differences in SRP between the lake and the two treatment enclosures. In the early summer the turnover time of phosphorus in the lake was rapid, indicative of a high phosphorus demand. The June 29 sample had a turnover time of 3.3 min. This extremely fast turnover time occurred during a period when the water was opalescent. On June 29 the +N enclosure was also opalescent and the phosphate turnover time was less than 1.5 min. The opalescence was observed at other periods of low phytoplankton growth, both in the lake and in the +P enclosure. The opalescence is best explained as a carbonate precipitation. The opalescence was not associated with an increase in bacteria (J. Barica, unpublished data). The opalescence occurred at the highest observed pH, 9.0; thus, the carbonate concentration would be high and many carbonates would be supersaturated (Kelts and Hsu 1978). Calcium analysis on some preserved (freeze-dried) samples collected from Lake 885 in 1977 gave these

TABLE 5. $^{32}PO_4$ turnover times for Lake 885 in 1977.

	L 885		L 885 +P		L 885 +N	
Date	SRP[a]	tt[b]	SRP	tt	SRP	tt
June 15	4	14	34	670	8	46
June 29	9	3.3	57	1440	5	<1.5
July 13	5	21	211	2700	95	long
July 26	7	280	235	4800	4	7.4
Aug. 3	8	67	71	—	71	1160
Aug. 16	4.5	84	85	3500	15	760

[a]Soluble reactive phosphorus in $\mu g\ P \cdot L^{-1}$.
[b]Turnover time of $^{32}PO_4$ in minutes.

values: June 15, 51.6 ± 0.1 mg $Ca \cdot L^{-1}$; July 8, 13.3 ± 0.1 mg $Ca \cdot L^{-1}$; Aug. 4, 9.9 ± 0.1 mg $Ca \cdot L^{-1}$. Although we only have results for three dates, they show that most of the calcium precipitated from the water column during the period coinciding with rapid PO_4 turnover in the lake (June 29). There is a large seasonal change in the calcium and carbonate concentrations of Lake 885, suggesting that it is calcium carbonate that precipitates (summer, 38.7 mg $Ca \cdot L^{-1}$, 380 mg $HCO_3 \cdot L^{-1}$, 37 mg $CO_3 \cdot L^{-1}$; winter 52.3 mg $Ca \cdot L^{-1}$, 592 mg $HCO_3 \cdot L^{-1}$; Barica 1975a).

Although carbonates are known to precipitate in prairie lakes (Schwartz and Gallup 1978), there has not been a study of the effect of carbonate precipitation on the availability of phosphorus or on algal growth in these lakes. The carbonate precipitation would occur once the water was warm and once the algal productivity had increased the pH. A period of calm weather in a bloom period could result in a highy stratified water column and rapid carbonate precipitation.

In another study, Murphy et al. (1983) observed that calcite precipitation appeared to remove phosphorus from the water column. Thus, it is highly probable that the carbonate precipitation in Lake 885 would lead to a period of phosphorus limitation. The algae would start to lyse, resulting in the observed high levels of ammonia which are periodically lost in storms by volatilization (Murphy and Brownlee 1981a). The volatilization then results in a period of nitrogen limitation which initiates nitrogen fixation. The importance of carbonate precipitation in setting up the instability of the nitrogen cycle in these eutrophic prairie lakes should be further evaluated.

This sequence of events complements the observation that bloom collapses are associated with changes in weather but that the bloom collapse can precede the deterioration of weather conditions by a day or two (Papst et al. 1980). This hypothesis also explains why not all adverse changes in weather result in a bloom collapse. If the algae have been subjected to severe phosphate limitation by a calcite coprecipitation of phosphate, the algae may not be vigorous enough to survive a period of poor light.

Acknowledgments

We thank Drs J. Barica, G. B. Ayles, and J. Mathias for their support and for providing facilities at Erickson. The interest and cooperation of M. Papst and J. Lark is appreciated. Mrs K. Edmondson assisted with field experiments and very capably performed the ^{15}N and particulate nitrogen analyses. We thank Drs D. R. S. Lean and B. K. Burnison for reviewing the manuscript.

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Electrophoretic Identification of *Sebastes* and *Helicolenus* in the Northwestern Atlantic

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An electrophoretic survey of 16 enzymes was conducted on representatives of the genera *Helicolenus* sp. and *Sebastes* spp. The survey was designed to develop an identification scheme for the commercially exploited species, because in the absence of any detailed description of their geographic distribution in the Scotian Shelf, they are currently managed as a single unit. Twelve enzymes were diagnostic for *H. dactylopterus*, three were diagnostic for *S. fasciatus*, while on the basis of the mobility of the most common allele none of the enzymes examined could distinguish between *S. mentella* and *S. marinus*. A protocol for the identification of *S. fasciatus* is thus presented, which incorporates the results of this survey. It is also suitable to describe the geographic distribution of commercially important species. The electrophoretic identification of the *Sebastes* species allowed fish with intermediate meristic characters, such as the number of anal fin rays, to be unequivocally identified. It was concluded that generic separation of *Helicolenus* and *Sebastes* is warranted, that *S. fasciatus* is distinct from *S. marinus* and *S. mentella*, but that individuals of *S. marinus* and *S. mentella* cannot be differentiated electrophoretically.

McGLADE, J. M., M. C. ANNAND, AND T. J. KENCHINGTON. 1983. Electrophoretic identification of *Sebastes* and *Helicolenus* in the northwestern Atlantic. Can. J. Fish. Aquat. Sci. 40: 1861 – 1870.

Un relevé électrophorétique de 16 enzymes a été effectué sur des représentants des genres *Helicolenus* sp. et *Sebastes* spp. Le but de cette étude était de mettre au point un système d'identification des espèces exploitées commercialement et qui, actuellement, par suite du manque de description détaillée de leur distribution géographique sur le plateau Scotian, sont gérées comme une unité. Douze enzymes sont diagnostiques de *H. dactylopterus*, trois le sont de *S. fasciatus*, tandis que, sur la base de la mobilité de l'allèle le plus commun, aucune des enzymes étudiées ne permet de séparer *S. mentella* et *S. marinus*. Nous décrivons donc une méthode d'identification de *S. fasciatus*, incorporant les résultats de la présente étude. La méthode permet également de préciser la distribution géographique des espèces d'importance commerciale. Grâce à l'identification électrophorétique des espèces de *Sebastes*, les poissons possédant des caractères méristiques intermédiaires, tels que le nombre des rayons de la nageoire anale, peuvent être identifiés sans équivoque. Nous concluons que la séparation des genres *Helicolenus* et *Sebastes* est justifiée, que *S. fasciatus* est distinct de *S. marinus* et de *S. mentella*, mais que des exemplaires de *S. marinus* et *S. mentella* ne peuvent être différenciés électrophorétiquement.

Received March 1, 1983
Accepted July 8, 1983

Reçu le 1 mars 1983
Accepté le 8 juillet 1983

THE northwestern Atlantic Sebastinae (Scorpaenidae) include three commercially important redfishes of the genus *Sebastes* (*S. fasciatus*, *S. marinus*, and *S. mentella*), and one rosefish of the genus *Helicolenus* (*H. dactylopterus*), which although related, is not commercially exploited because of its small size (Robins et al. 1980). The morphological similarity among these fishes is such that they cannot be consistently identified in the field: this in turn has precluded any definitive analysis of their biology and distribution. Thus, redfish in the northwestern Atlantic are treated as a single entity by fisheries management. However, the ramifications of such an approach

Printed in Canada (J7276)
Imprimé au Canada (J7276)

are very serious, as any one of the species may become differentially exploited (Kenchington 1982). In conclusion, there is an urgent need to confirm the taxonomic status of the *Sebastes* spp., and to develop unequivocal identification methods for them.

The blackbelly rosefish, *H. dactylopterus* (Da la Roche 1809) syn. *H. dactylopterus dactylopterus* (Eschmeyer (1969), and *H. dactylopterus maderensis* (Barsukov 1979)) is a southern species found along the Atlantic coast from the Scotian Shelf, southward to Virginia (Leim and Scott 1966; Musick 1966; Halliday and Scott 1969; Kenchington 1980). Its size range and general morphology are such that adults can be confused with juvenile *Sebastes*. The putative *Sebastes* species are: (1) *S. fasciatus* Storer 1854, a shallow-water form (syn. *S. viviparus* (Gill 1863), and the "American form" of *S. marinus* type *mentella* (Templeman 1959), equivalent to *S. fasciatus* and described by Barsukov (1968)); (2) *S. marinus* (L.) a more northern and eastern form (syn. *S. norvegicus* (Cuvier and Valenciennes 1829)); and (3) a deepwater form, *S. mentella* Travin 1951. To avoid confusion in this paper, we refer to the three groups as distinct species.

There have been numerous studies of the organismal differences among the *Sebastes* spp. and their European congener *S. viviparus*. These have examined meristic and morphometric characters (e.g. Travin 1951; Barsukov 1972; Barsukov and Zakharov 1972; Litvinenko 1974; Ni 1981a), internal musculature (Hallacher 1974; Litvinenko 1980; Ni 1981b; Power and Ni 1982), larval characteristics (Templeman and Sandeman 1959; Moser et al. 1977; Templeman 1980) and parasites (Sindermann 1961; Yanulov 1962a, 1962b). At the cellular and molecular levels there have been studies of immunological and chromatographic characteristics (O'Rourke 1961), and of free amino acid concentrations (Schaefer 1961), tests on the thermostability of particular cells (Altukhov et al. 1968a, 1968b), and analyses of electrophoretic variation (Johnson et al. 1971; Tsuyuki et al. 1968; Altukhov 1981; Altukhov and Nefyodov 1968; Naevdal 1978; Nefyodov 1971; Payne and Ni 1982). In all, the results show that *S. viviparus* can be distinguished from all other *Sebastes* spp., that *S. fasciatus* and *S. mentella* appear superficially the most similar, but that *S. marinus* and *S. mentella* are closest genetically and morphologically. However, none of these studies have been able to demonstrate unequivocal criteria to separate *S. fasciatus* from *S. mentella* or *S. marinus*.

The two characters currently used to separate the *Sebastes* spp. are the number of anal fin rays (Ni 1981a) and the passage of the extrinsic gas-bladder muscles between the ribs (Ni 1981b). Yet the anal fin ray count has an overlapping distribution in all three *Sebastes* spp., and range of rib position for the passage of the extrinsic gas-bladder muscle appears nonoverlapping but adjacent in *S. fasciatus* and *S. mentella* (Ni 1981a, b), and intermediate in *S. marinus*. Moreover, the genetic bases of these characters are unknown.

Electrophoresis coupled with histochemical staining, allows the visualization and interpretation of banding patterns as gene products (Allendorf and Utter 1979). Thus the extent of genetic variation between individuals of putative species can be examined, and used to establish the relationships between different taxa (Avise 1974).

This paper presents the results of an electrophoretic survey of representatives of the four redfish and rosefish species found in the northwestern Atlantic, as the first phase in providing an efficient and effective method of identification. The study demonstrates the ability of electrophoresis to separate *H. dactylopterus* from *Sebastes* spp. unequivocally, and more importantly, *S. fasciatus* from its congeners. The protocols suggested herein for such routine identification of *S. fasciatus* and *S. mentella* have been tested and shown to be successful in a large sample of redfish from an alternative area (to be presented elsewhere).

Materials and Methods

A blind study was conducted on adult redfish, in which samples were identified by morphological criteria but labeled only by number for the electrophoretic analyses. The redfish were obtained from the eastern part of the Scotian Shelf, from bottom trawl catches taken by the R.V. *Lady Hammond* during March, 1982 (Table 1). *S. fasciatus* and *S. mentella* were sorted by anal fin ray counts, following Barsukov and Zakharov (1972): fish with 6 or 7 anal rays were labeled *S. fasciatus*, those with 9 or 10 were labeled as *S. mentella*, and those with 8 were labeled as "unknown." Ten fish of each group were collected. Identification of *S. marinus* and *H. dactylopterus* followed the methods of Templeman (1959), Barsukov and Zakharov (1972), Bigelow and Schroeder (1953), and Leim and Scott (1966). Samples of heart, muscle, and liver were removed from each fish, and immediately frozen at −20°C: upon return to port, the samples were transferred to a freezer and kept at −40°C. The *S. fasciatus*, *S. mentella*, and "unknowns" were measured and subsequently dissected, and their extrinsic gas-bladder muscle routes determined using Hallacher's (1974) method (Kenchington 1983).

Each tissue sample was mechanically homogenized in twice its volume of cold distilled water and centrifuged at 3090 × *g* at 4°C for 15 min. Vertical and horizontal gel electrophoresis of the supernatant fractions were then carried out in a 12% starch solution following the methods of Smithies (1959), Odense et al. (1978), and May et al. (1979). Agarose isoelectric focusing (IEF) of *S. fasciatus* and *S. mentella* muscle extracts was also undertaken using Lundstrom's (1981) method.

Three buffer systems were used:

Buffer A — Amine citrate pH 6.9 (Clayton and Tretiak 1972).
Gel: 0.002*M* citric acid (*M* = mol/L), adjusted to pH 6.9 with *N*-(3-aminopropyl)-diethanolamine.
Electrode: 0.04*M* citric acid, adjusted to pH 6.9 as above.

Buffer B — Tris EDTA borate pH 8.7 (Odense and Leung 1975).
Gel and electrode: 121 g tris, 12 g EDTA and 9.2 g boric acid in 2 L; diluted 1:3 with distilled water.

Buffer C — Discontinuous tris citric acid (Ridgway et al. 1970).
Gel: (pH 8.5) 0.03*M* tris, 0.005*M* citric acid,

TABLE 1. Location and depth of sets from which fish samples were taken on the R.V. *Lady Hammond* (cruise H073).

Set No.	Latitude	Longitude	Depth (m)	Species present[a]
2	43°30.31′	59°52.17′	282	*S. mentella*
6	43°46.47′	58°59.88′	275	*S. mentella* *S. fasciatus*
11	44°09.94′	59°25.57′	103	*S. fasciatus*
20	44°13.42′	59°05.02′	133	*S. fasciatus*
24	43°59.33′	58°31.26′	220	*S. mentella* *S. fasciatus*
31	44°20.82′	57°33.26′	95	*S. marinus*
65	43°25.05′	60°18.01′	136	*H. dactylopterus*
88	42°51.91′	63°20.83′	87	*H. dactylopterus*
89	42°48.70′	63°22.92′	114	*H. dactylopterus*
90	42°47.72′	63°46.89′	170	*H. dactylopterus*

[a]Based on anal fin ray counts, extrinsic gas-bladder muscle routes and subsequently identified using the results of this study.

0.0006*M* lithium hydroxide, 0.003*M* boric acid.

Electrode: (pH 8.5) 0.06*M* lithium hydroxide, 0.3*M* boric acid.

The starch gels were approximately 8 mm deep. Fifteen tissue extracts were placed in slots on each gel, and the gels run for either 16 h (LDH, MDH, and IDH) or 6 h in a cold room kept at 1°C. Gels made with buffer A were run at 25mA, and 280−300V, those with buffer B at ≤45mA, and those with buffer C at 50mA. Each gel was cut twice, and the slices stained according to modifications in the recipes of Shaw and Prasad (1970). A summary of enzymes, buffers and stains is given (Table 2). The observed banding patterns were assigned genotypes as described by May (1980). Allelic nomenclature follows that of Allendorf and Utter (1979), May et al. (1979) and May (1980), in which loci are numbered sequentially from the cathode to the anode. Those in the cathodal region are preceded by a negative sign. The most common allele is designated 100, and all others are labeled by their migratory ratio to the common allele. In cases where variation cannot be assigned to any one locus, the format changes to include all loci, with their appropriate gene dosages in sequential order. The IEF gel was based on a 1.6% solution of agarose using LKB (LKB-Produkter AB, Bromma, Sweden) ampholytes to produce a pH range of 3−10, and run with an LKB Multiphor. The gel was stained for total protein using a 4:2:4, methanol:acetic acid:water solution of 0.04% Serva Violet 49B (modified from Lundstrom (1981)).

Results

Of the 16 enzymes electrophoretically surveyed, 14 could be scored routinely. The number of presumptive loci which could be observed consistently was 25. The tissues associated with each locus (Table 2) are those for which the protein was actually scored; however activity often occurred in other tissues. Similarly, while the electrophoretic environment cited in Table 2 was the one which produced the clearest separation of the various bands, activity was observed under a range of electrophoretic conditions.

Alcohol dehydrogenase (1.1.1.1)

The banding patterns observed for alcohol dehydrogenase suggested that there was activity at two loci; one in the heart and liver (*ADH*-1), and another in the muscle (*ADH*-2) in *Sebastes*, and one in the liver (*ADH*-1), and another in the heart and muscle (*ADH*-2) in *Helicolenus*. Alternate alleles, giving a three-banded pattern in the heterozygous condition, were observed for *ADH*-1 locus in *S. fasciatus* and *H. dactylopterus*. The common alleles for both loci in each member of the *Sebastes* group had the same mobilities; that of *ADH*-1 in *H. dactylopterus* was more anodal. *ADH*-1 was consistently cathodal with buffer A, whilst *ADH*-2 was anodal (Fig. 1).

Octanol dehydrogenase (1.1.1.1)

Activity was observed in liver extracts for this protein; however, the resolution was insufficient to score the gene products.

α-Glycerophosphate dehydrogenase (1.1.1.8)

Two loci were scored for this protein; *αGP*-1 from muscle tissue and *αGP*-2 from liver tissue. For both systems, the homozygotes have one major band, which is cathodal in *Sebastes* and anodal in *H. dactylopterus* in gels made with buffer A. An alternate allele was scored for *S. marinus* for *αGP*-1 giving a three-banded heterozygote. In addition to each major band several weak, more anodal, satellite bands were observed for all species (Fig. 1). The patterns observed for *αGP*-1 in both *H. dactylopterus* and *S. marinus*, agree with those given by Johnson et al. (1970, 1971, 1972, 1973). Separation amongst the *Sebastes* spp. on the basis of the most common allele was not possible with αGP.

Sorbitol dehydrogenase (1.1.1.14)

Two loci were scored in both heart and liver tissues in all the species examined. Polymorphic loci were found in *S. mentella* and *S. marinus* for *SDH*-1. Homozygotes were characterized by two bands, while heterozygotes for *SDH*-1 showed the five major bands expected for a tetramer. The mobilities of the most common alleles were clearly different between the two genera, and between *S. fasciatus* and the other two *Sebastes* spp. (Fig. 1, 2a): thus this enzyme is considered diagnostic for *S. fasciatus* and *H. dactylopterus*.

Lactate dehydrogenase (1.1.1.27)

A single invariant band was observed at the same anodal position, for each tissue in all species, as previously reported (Johnson et al. 1972; Payne and Ni 1982). However, eye extracts, which were unavailable for this analysis, could yield more information on the genetic structure of this enzyme.

Malate dehydrogenase (1.1.1.37)

At least 5 loci encode for this protein; the banding patterns obtained suggest that there are two monomorphic, mitochondrial forms and 3 supernatant forms. In this study only the

TABLE 2. Enzymes (recommended names, abbreviations, and E.C. number), buffers and staining solutions used; H = heart, L = liver, M = muscle.

Enzyme	Tissue	Number of loci scored	Buffer	Stain buffer	Staining solution
Alcohol dehydrogenase	H,L	1	A	Tris HCl	2 mg PMS 25 mg NBT 10 mg NAD
ADH (1.1.1.1)	M	1		pH 8.0	5 mL ethanol — 95%
Octanol dehydrogenase	L	0	A	Tris HCl	2 mg PMS 25 mg NBT 10 mg NAD
ODH (1.1.1.1)				pH 8.0	5 mL octanol
α-Glycerophosphate dehydrogenase	M	1	A	Tris HCl	2 mg PMS 25 mg NBT 10 mg NAD
αGP (1.1.1.8)	L	1		pH 8.0	2 g sodium α-glycerophosphate
Sorbitol dehydrogenase	H,L	2	A	Tris HCl	2 mg PMS 8 mg MTT 10 mg NAD
SDH (1.1.1.14)				pH 8.5	D-sorbitol 300 mg
Lactate dehydrogenase	H,M,L	1	A	Tris HCl	2 mg PMS 25 mg NBT 10 mg NAD
LDH (1.1.1.27)				pH 8.0	7 mL 10% lactic acid
Malate dehydrogenase	H,M	4	A	Tris HCl	2 mg PMS 25 mg NBT 10 mg NAD
MDH (1.1.1.37)	H,L	1		pH 10.0	7 mL 0.2*M* malic acid
Malic enzyme	H,M,L	0	A	Tris HCl	2 mg PMS 25 mg NBT 10 mg NADP
ME (1.1.1.40)				pH 10.0	7 mL 0.2*M* malic acid
Isocitrate dehydrogenase	H,M	1	A	Tris HCl	10 mg PMS 20 mg NBT 10 mg NADP
IDH (1.1.1.42)	L	1		pH 8.0	200 mg M_gCl_2 100 mg isocitric acid
6-Phosphogluconate dehydrogenase	H,L	1	B	Tris HCl	1 mg PMS 15 mg NBT 10 mg NADP
6PG (1.1.1.44)				pH 7.0	50 mg phosphogluconic
Galactose dehydrogenase	L	1	A	Tris HCl	2 mg PMS 25 mg NBT 50 mg NAD
GAL (1.1.1.48)				pH 8.5	1.8 g galactose
Peroxidase	L	1	C	0.5% glacial acetic	200 mg benzidine dihydrochloride
PER (1.11.1.17)					0.2 mL 30% H_2O_2
Superoxide Dismutase	L	2	C	Tris HCl	10 mg NBT 2 mg PMS
SOD (1.15.1.1)				pH 8.5	
Amino aspartate transferase	M,L	2	B	Transac substrate[a]	3 transac color developing tablets
AAT (2.6.1.1)				pH 7.4	
Phosphoglucomutase	H,M,L	1	C	Tris HCl	1 mg PMS 5 mg MTT 5 mg NADP 80 mg G-1-PK_2 $4H_2O$
PGM (2.7.5.1)	L	1		pH 8.0	1 mg G-1-6DiP 300 mg M_gCl_2 $6H_2O$ 20 units G6PDH
Esterase	H,M	2	B	Tris maleate	200 mg fast blue RR salt 150 mg α-naphthyl acetate in
EST (3.11.1)				pH 6.0	2 mL acetone
Phosphoglucose isomerase	L	2	C	Tris HCl	1 mg PMS 5 mg MTT 8 mg NADP
PGI (5.3.1.9)				pH 8.0	20 mg F6PDiNa 20 units G6PDH

[a]Transaminase reagent general diagnostics division Warner Chilcott Labs. Morris Plains, NJ.

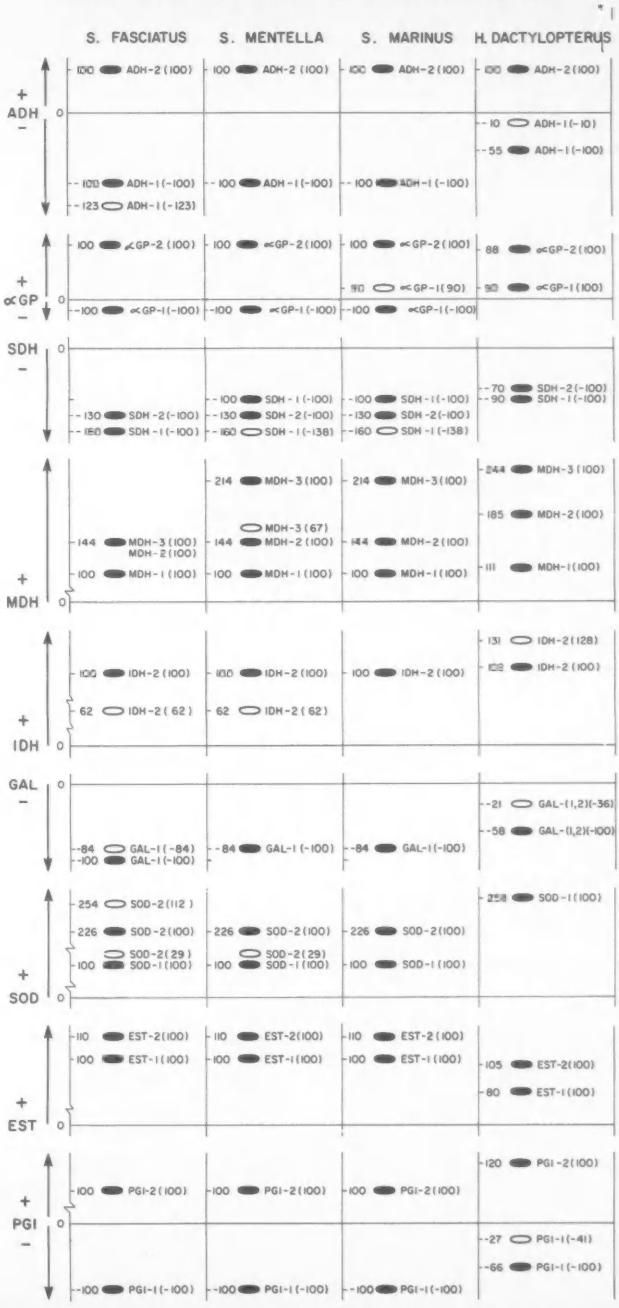
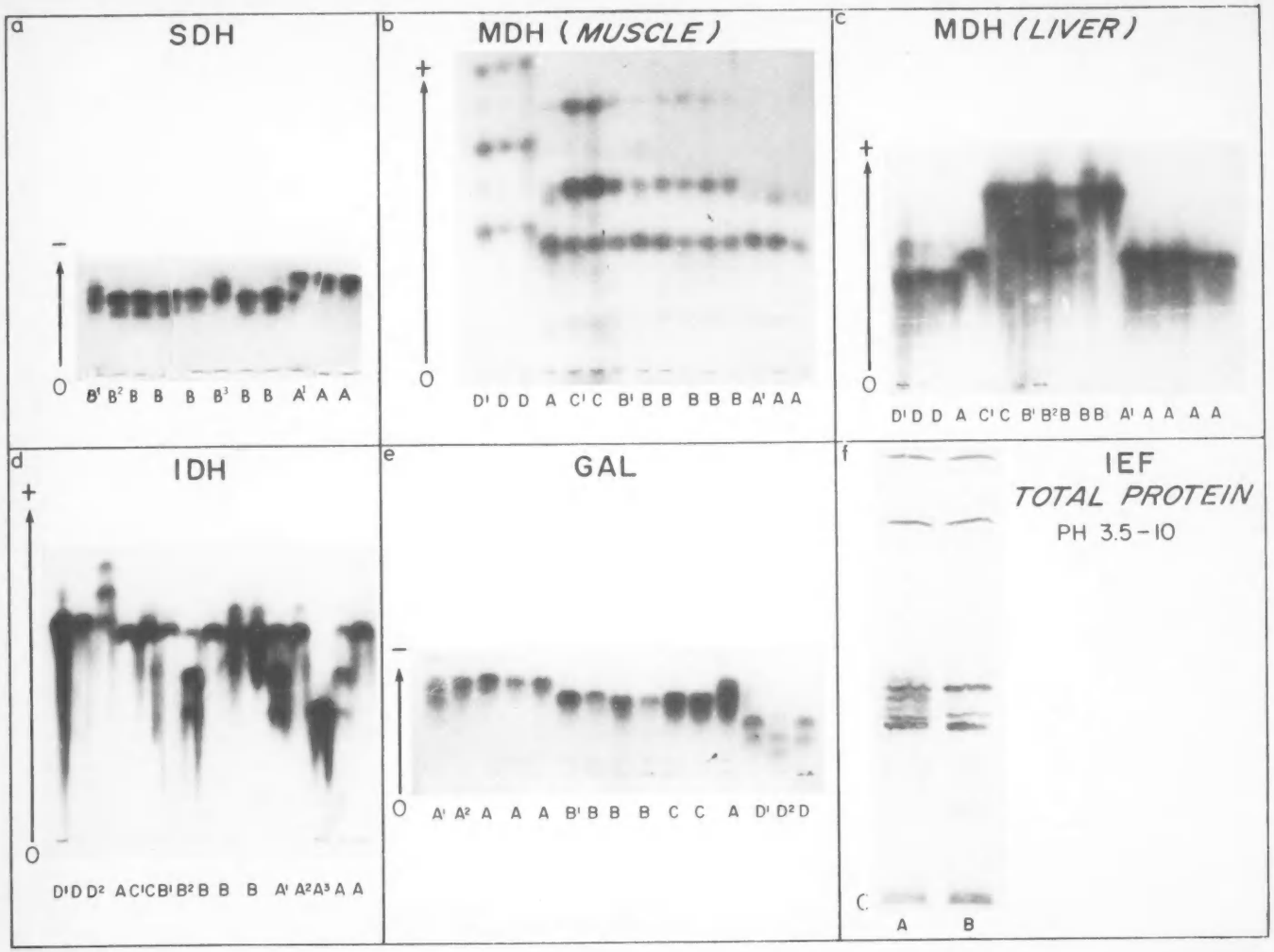


FIG. 1. Electrophoretic mobilities of enzymatic allelic products in *Sebastes* spp. and *Helicolenus* sp. Diagrammatic representations of electromorphs represent relative mobilities and do not include heterozygotes. The most common allelic products are indicated by solid symbols; those seen in only one or two individuals are indicated by open symbols.


a
SDH
B¹ B² B B B B³ B B A¹ A A
b
MDH (MUSCLE)
D¹ D D A C¹ C B¹ B B B B B A¹ A A
c
MDH (LIVER)
D¹ D D A C¹ C B¹ B²B BB A¹ A A A A
d
IDH
D¹D D² AC¹CB¹B²B B B A¹ A²A³ A A
e
GAL
A¹ A² A A A B¹ B B B C C A D¹ D²D
f
IEF
TOTAL PROTEIN
PH 3.5 – 10
A B

latter were scored. Amongst the *Sebastes* spp., *MDH*-1 and *MDH*-2 were resolved most clearly in heart and muscle extracts (Fig. 2b), and *MDH*-3 in heart and liver (Fig. 2c). The mobilities of *MDH*-1 and *MDH*-2 were the same for all the *Sebastes* spp. In *S. fasciatus*, activity of the alleles for *MDH*-3 had the same mobility as those for *MDH*-2. In *S. mentella*, an alternate allele was observed for *MDH*-3; heterozygotes showed a three-banded pattern of activity rather than the six observed in other species (Ward and Beardmore 1977; May 1980).

In *H. dactylopterus*, *MDH*-1 was scored from extracts of the heart, muscle and liver, whereas *MDH*-2 and -3 were scored only from muscle extracts. Thus, in Fig. 2b the band associated with *MDH*-1 in *H. dactylopterus* is slightly cathodal to *MDH*-3 in liver extracts of *Sebastes* spp. This enzyme is considered to be diagnostic of *S. fasciatus*, and *H. dactylopterus*.

Malic enzyme (1.1.1.40)

Activity for this enzyme was very weak in all extracts, thus information concerning its structure cannot be presented.

Isocitrate dehydrogenase (1.1.1.42)

The stained products of this enzyme suggest that it is encoded by two loci: *IDH*-1 in heart and muscle, and *IDH*-2 in liver. Heterozygotes gave three banded patterns, and were observed at the *IDH*-2 locus in *S. mentella*, *S. fasciatus* and *H. dactylopterus*. The allelic mobilities for *IDH*-1 and *IDH*-2 were identical for all the *Sebastes* spp., whilst those for *H. dactylopterus* were more anodal (Fig. 2d).

6-Phosphogluconate dehydrogenase (1.1.1.44)

A single invariant band was observed in heart and liver extracts of the *Sebastes* spp., as reported by Payne and Ni (1982). In *H. dactylopterus* fast and slow alleles were identified, the heterozygote of which produced a three-banded phenotype.

Galactose dehydrogenase (1.1.1.48)

The banding patterns in extracts of liver from *H. dactylopterus* suggest that this enzyme is a dimer coded by two loci which share the same, electrophoretically distinct, alleles. In *Sebastes* spp., however, the patterns obtained in extracts of liver suggest a single locus which produces three-banded heterozygotes. The enzyme was scored on gels made with both buffers A and C; the latter produced gene products which stayed at or close to the origin, whereas on gels made with buffer A, the gene products were entirely cathodal. The common allelic bands in *S. fasciatus* were more cathodal than their homologues in *S. mentella* and *S. marinus*, whereas the alternate alleles, observed in *S. fasciatus* and *S. mentella*, had the same mobilities as their counterpart's common allele. The common and alternate alleles for *GAL*-1, and 2 in *H. dactylopterus* were less cathodal than in *Sebastes* spp. Heterozygotes in *H. dactylopterus* produced three-banded patterns with 9:6:1 and 1:2:1 configurations (Fig. 2e). This enzyme is thus diagnostic for *H. dactylopterus* and *S. fasciatus*.

Peroxidase (1.11.1.17)

One locus was scored for this enzyme, using buffer C; the gene products were an invariant, slightly cathodal band in the *Sebastes* spp. and a single invariant, anodal band in *H. dactylopterus*.

Superoxide dismutase (1.15.1.1)

This enzyme appears on gels stained for GAL, ADH, SDH, and GP. It occurs in the liver and heart and is best resolved with buffer C. Two loci were postulated for the *Sebastes* spp. and one for *H. dactylopterus*; the latter observation agrees with the findings of Johnson et al. (1972). Alternate alleles were observed for *SOD*-2 in *S. fasciatus* and *S. mentella*, for which three-banded heterozygotes were observed. No alternate alleles were seen in *S. marinus* and *H. dactylopterus*. The mobilities of the common alleles distinguish *H. dactylopterus* from the *Sebastes* spp.

Amino aspartate transferase (2.6.1.1)

One locus was scored for this enzyme from extracts of liver; another more anodal band was assumed to be a supernatant form (Avise and Selander 1972; Ward and Beardmore 1977). An alternate allele was observed for *AAT*-1 in *H. dactylopterus*, corresponding to the VS allele in Johnson et al. (1971). The heterozygote was three-banded, indicating that AAT in redfish acts as a dimer, as in other species for which it has been recorded (Ward and Beardmore 1977; May 1980). The mobility of the most common allele for *AAT*-1 in *H. dactylopterus* was less anodal than those of the *Sebastes* spp. and is thus considered diagnostic.

Phosphoglucomutase (2.7.5.1)

Our results of staining for this enzyme confirm Johnson

FIG. 2. Representative phenotypes for enzymes in redfish: A = *S. fasciatus*, B = *S. mentella*, C = *S. marinus*, and D = *H. dactylopterus*: a) B^1 = *SDH*-1 (−100/−100/−160/−160); B^2 = *SDH*-1 (−100/−100/−100/−100), A^3 = *SDH*-1 (−160/−160/−160/−160), A^1 = *SDH*-1 (−100/−100/−100/−100), for all examples *SDH*-2 = (−100/−100/−100/−100); b) A^1 = *MDH*-1 (100/100), *MDH*-2 (100/100), *MDH*-3 (100/100), B^1 = *MDH*-1 (100/100), *MDH*-2 (100/100), *MDH*-3 (100/100), C^1 = *MDH*-1 (100/100), *MDH*-2 (100/100), *MDH*-3 (100/100), D^1 = *MDH*-1 (100/100), *MDH*-2 (100/100), *MDH*-3 (100/100); c) A^1 = *MDH*-2 (100/100), *MDH*-3 (100/100), B^1 = *MDH*-2 (100/100), *MDH*-3 (100/100), B^2 = *MDH*-2 (100/100), *MDH*-3 (100/67), C^1 = *MDH*-2 (100/100), *MDH*-3 (100/100), D^1 = *MDH*-1 (100/100); d) A^1 = *IDH*-2 (100/62), A^2 = *IDH*-2 (100/100), A^3 = *IDH*-2 (62/62), B^1 = *IDH*-2 (100/100), B^2 = *IDH*-2 (100/62), C^1 = *IDH*-2 (100/100), D^1 = *IDH*-2 (100/100), D^2 = *IDH*-2 (100/128); e) A^1 = *GAL*-1 (−100/−84), A^1 = (−100/−100), B^1 = *GAL*-1 (−100/−100), C^1 = *GAL*-1 (−100/−100), D^1 = *GAL*-1,2 (−100/−100/−100/−36), D^2 = *GAL*-1,2 (−100/−100/−36/−36); f) Isoelectric focusing gel stained for total protein, to show the difference between *S. fasciatus* and *S. mentella*.

TABLE 3. Diagnostic (+) and nondiagnostic (−) enzymes amongst the four redfish species examined.

Species	AAT	ADH	αGP	EST	GAL	IDH	MDH	POR	6PG	PGI	SDH	SOD
H. dactylopterus	+	+	+	+	+	+	+	+	+	+	+	+
S. marinus	−	−	−	−	−	−	−	−	−	−	−	−
S. mentella	−	−	−	−	−	−	−	−	−	−	−	−
S. fasciatus	−	−	−	−	+	−	+	−	−	−	+	−

et al.'s (1972) in that the gene products were derived from two polymorphic loci. This enzyme was resolved only for *S. fasciatus* and *S. mentella*. *PGM*-1 was present in the heart, muscle and liver of these two species, contrary to its sole occurrence in the muscle of *Sebastodes alutus* (Johnson et al. 1971); *PGM*-2 was present in the liver. Homozygotes were single banded and heterozygotes were two-banded, which suggests that this enzyme acts as a monomer. The mobilities of the common and alternate alleles were the same for these two species on gels made with buffers A and C. Variability at the *PGM*-2 locus in liver extracts was observed with buffer C, but could not be consistently scored.

Esterase (3.11.1)

The esterases scored in this survey were those with activity towards α-naphthyl acetate, which in fishes generally behave as monomers (Ward and Beardmore 1977). Activity was observed in liver, muscle, and heart extracts: however, the liver esterases could not be adequately resolved in the course of this study. Hence loci were assigned only to the muscle and heart esterases. *EST*-1 in muscle had the same mobility in all *Sebastes* spp., but in *H. dactylopterus* it was distinctly less anodal. *EST*-2 in muscle and heart had the same mobility for all *Sebastes* spp., and was slightly less anodal in *H. dactylopterus*.

Phosphoglucose isomerase (5.3.1.9)

Two loci were scored from the banding patterns produced by liver extracts on gels made with buffer C. In both cases the homozygotes were single banded, whilst for *PGI*-1 in *H. dactylopterus* the heterozygotes were three-banded, suggesting that this enzyme is a dimer. The mobilities of all the gene products of *PGI*-1 were identical for all *Sebastes* spp., and slightly less cathodal in *H. dactylopterus* (Fig. 1).

Isoelectric focusing gels

The results of staining the IEF gels for total proteins showed a clear difference in the number and position of bands in *S. fasciatus* and *S. mentella* (Fig. 2f). The deposition of these bands was invariant in all the cases observed.

Systematic diagnoses

In *H. dactylopterus*, the mobility of all loci for 12 of the 16 enzymes surveyed were distinct from those of the *Sebastes* spp. (Table 3). In *S. fasciatus*, 3 enzymes (MDH, GAL, and SDH), were diagnostic, in that they could distinguish it from its congeners. Alternate alleles for SDH and αGP were found in *S. mentella* and *S. marinus* respectively; however, on the basis of the mobility of the most common allele these two species could not be distinguished. Total protein patterns deposited on agarose IEF gels, differentiated between *S. fasciatus* and *S. mentella*.

When the results of the blind study were matched up with the morphological dissection, the 10 "unknown" fish (viz. those with 8 anal fin rays) were classified; 3 were *S. mentella*, and 7 *S. fasciatus*. One fish which had originally been identified as *S. marinus* based on external criteria, was reidentified as *S. fasciatus*, from its electrophoretic profile. All the other identifications were congruent. Thus, the electrophoretic criteria derived above, were diagnostic for both genera, and for the separation of *S. fasciatus* from *S. marinus* and *S. mentella*.

Discussion

The advantage of using biochemical characters to identify species is that they can provide a genetic base for observed organismal differences. In this case inheritance studies were not available; however, the observed phenotypes for each enzyme fitted known or postulated models in other fishes. Thus our results have been placed in the context of putative genotypes, rather than simple "band-counting." The only exceptions to this were the isoelectric focusing gels, in which the banding patterns were too complex to suggest a simple, unequivocal, genetic model, but nevertheless could be used to separate species of the same genus.

A comparison of phenotypes at the generic level shows that *Helicolenus* and *Sebastes* have only two enzyme profiles in common (LDH and PGM); this result agrees with that of Johnson et al. (1972) even though they only surveyed 7 enzymes. Tsuyuki et al. (1968) and Johnson et al. (1972) further suggest that the Atlantic and Pacific *Sebastes* are more similar to each other than either is to any of the other genera studied. The results of this study would indicate that *Helicolenus* and *Sebastes* are clearly more divergent than the species within the *Sebastes* group.

At the infrageneric level, *S. fasciatus* appears quite distinct from its congeners. At three loci (*MDH*-3, *GAL*-1, and *SDH*-1) this species has a fixed or common allele that is different from either *S. mentella* or *S. marinus*. This result has been corroborated by a survey of over 1000 redfish from the Gulf of St. Lawrence, in which the frequency of the alternate alleles was much less than 1% (unpublished data). The only comparable data are those of Payne and Ni (1982): they surveyed 8 enzymes, 7 of which are included here. In their work, Payne and Ni did not observe any polymorphic loci for PGM, and observed different gene frequencies for *MDH*-3 and *SOD*-2 compared to those given in this study.

However, the sample sizes in both studies are too small to be conclusive. Payne and Ni scored esterases with activity towards both naphthyl and methylumbelliferyl acetate, but concluded that the gene frequencies were not diagnostic.

Very little difference was observed between *S. marinus* and *S. mentella* except for the frequency of alternate alleles, which agrees with Altukhov and Nefyodov's work on cell thermostability and agar gel electrophoresis of blood serum (Altukhov and Nefyodov 1968; Nefyodov 1968, 1971; Altukhov 1974, 1981; Altukhov and Salmenkova 1981), Payne and Ni (1982), and the studies of O'Rourke (1961) and Schaeffer (1961). Indeed our results support Barsukov and Zakharov (1972) in concluding that *S. marinus* and *S. mentella* are much more similar than either is to *S. fasciatus*.

The problem of identification of *S. fasciatus* and *S. mentella* has been addressed by this blind study, in that all specimen identifications were congruent with an extensive set of morphological characteristics otherwise required to identify the samples. Moreover, the success of the sampling protocol suggested viz. electrophoretic characterization of MDH and GAL or SDH from liver extracts, has been supported in more extensive surveys on the Scotian Shelf and in the Gulf of St. Lawrence (to be presented elsewhere). This in turn would support the thesis put forward by Avise (1974), that representatives of each taxon can be sufficient to identify discriminatory characteristics. Whilst the protocol given above would not yield a field technique, it could most certainly be used to establish the geographic distribution of the commercially exploited redfish species, and to confirm specific identification of individuals used in biological studies.

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Estimating Population Size from Relative Abundance Data Measured with Error[1]

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COLLIE, J. S., AND M. P. SISSENWINE. 1983. Estimating population size from relative abundance data measured with error. Can. J. Fish. Aquat. Sci. 40: 1871–1879.

A modified DeLury method to estimate fish population size from relative abundance data was developed. The method may be applied either with or without knowledge of the age composition of catch. In addition to estimating catchability coefficients, the technique accounts for error in the measurement of relative abundance. A general-purpose nonlinear regression subroutine was used to fit the model. The technique is demonstrated using Northeast Fisheries Center bottom trawl survey data as a measure of relative abundance. Fitting was carried out for four fish populations: Georges Bank and Southern New England yellowtail flounder (*Limanda ferruginea*); Georges Bank and NAFO SA 4X haddock (*Melanogrammus aeglefinus*). Catchability coefficients calculated in this manner are consistent with prior estimates. In addition, the technique smooths the survey data by filtering measurement error from true fluctuations in population size. Population size estimates for haddock derived by this method agree closely with virtual population analysis (VPA) estimates.

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Nous avons mis au point une modification de la méthode de DeLury pour estimer l'effectif de populations de poissons à partir de données sur l'abondance relative. Cette méthode peut être appliquée, que l'on connaisse ou non la composition par âge des prises. En plus d'estimer les coefficients de capturabilité, elle tient compte de l'erreur de mesure de l'abondance relative. Dans l'adaptation du modèle, nous avons utilisé une régression non linéaire à tous usages. Pour démontrer cette technique, nous faisons appel aux données recueillies par le *Northeast Fisheries Center* au cours de relevés au chalut de fond, comme mesure de l'abondance relative. Le modèle a été appliqué à quatre populations de poissons : la limande à queue jaune (*Limanda ferruginea*) du banc Georges et du sud de la Nouvelle-Angleterre; l'aiglefin (*Melanogrammus aeglefinus*) du banc Georges de la division SA de l'OPANO. Calculés de cette manière, les coefficients de capturabilité s'accordent avec des estimations antérieures. En outre, la méthode permet de lisser les données des relevés en séparant l'erreur de mesure des fluctuations réelles de l'effectif des populations. Les estimations d'abondance de l'aiglefin obtenues par cette méthode s'accordent bien avec celles de l'analyse de population virtuelle (VPA).

Received May 26, 1982
Accepted July 14, 1983

Reçu le 26 mai 1982
Accepté le 14 juillet 1983

DIRECT enumeration of a marine fish population over a large area is not generally possible; therefore, indirect methods of estimating population size are necessary. Standardized catch-per-unit-effort indices (based on either fishery or research vessel data) provide a measure of relative abundance; i.e. $n = qN$ where n is relative abundance, N is absolute population size, and q is a parameter called the catchability coefficient.

Catch-per-unit-effort data from commercial or recreational fisheries are difficult to standardize such that q is constant. Technological improvements increase fishing power and bias standardized indices. Therefore, standardized research vessel survey data are now broadly applied to monitor trends in population size (Clark 1979; Sissenwine et al. 1983).

Absolute abundance is determined by calibrating n (estimating q) using other independent information. One approach is to estimate the efficiency of sampling gear (i.e. q) by comparing survey catches with direct enumeration (using submersible or camera sleds, for example, Uzmann et al. 1977) within a relatively small area. Unfortunately, estimates of q for any specific area are not necessarily representative of a

[1]Woods Hole Oceanographic Institution Contribution No. 5083.

Printed in Canada (J6946)
Imprimé au Canada (J6946)

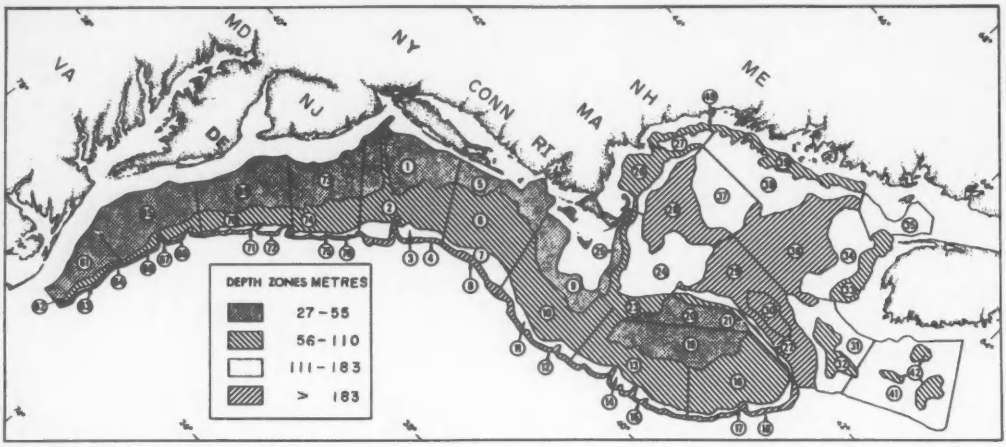

FIG. 1. NEFC bottom trawl survey strata.

much larger area inhabited by a population of fish.

Relative abundance is usually calibrated by comparison with virtual population analysis estimates (VPA; Gulland 1965; Pope 1972) of population abundance. Since relative abundance indices based on research vessel surveys suffer from inherent variability (Byrne et al. 1981), estimates of q are usually imprecise. Furthermore, VPA requires commercial catch-at-age data and is only useful for historic estimates of population size.

This paper introduces an alternate approach for estimating population size based on relative abundance indices and catch data. Two alternate forms of the model are developed. The first can be applied when only total catch is known; the second requires catch-at-age data. (Hereafter, the two forms of the model will be referred to as "non-age-structured" and "age-structured," respectively.) The technique makes use of DeLury's (1947) method as modified by Allen (1966).

Our method smooths the relative abundance indices by accounting for measurement variability in research vessel data. Statistically, this is the problem of structural relationship between variables (Kendall and Stuart 1973). The statistical method which we employ recently has been applied to the estimation of stock-recruitment relationships (Walters and Ludwig 1981; Ludwig and Walters 1981). Applied to relative abundance data, the technique estimates catchability coefficients and filters the survey data. Using this method, the total error is partitioned into observation error and variation not accounted for by the dynamic model. The filtering theory was developed by Kalman (1960) and applied to regression analysis by Duncan and Horn (1972). For this application the nonlinearity in the regression equations necessitates a numerical solution.

Data Base

Since 1963, the Northeast Fisheries Center (NEFC) has conducted standardized research vessel bottom trawl surveys during the autumn of each year along the northeast coast of the USA from just south of Hudson Canyon to Nova Scotia and from a depth of about 27 m to the edge of the continental shelf (Grosslein 1969; Clark 1979). In 1967, the survey area was extended southward to Cape Hatteras. A standard "36 Yankee" trawl with a 1.25-cm stretch-mesh cod-end lining has been used throughout the time series of autumn surveys. The trawl measures 24 m along the footrope, averages 3 m in height along the headrope, and is equipped with rollers to make it suitable for use on rough bottom.

Sampling has been based on a stratified random design. The survey area has been stratified into zones based on depth and latitude (Fig. 1). Approximately 300 stations are sampled during each survey although in recent years this number sometimes has been nearly doubled. Stations are allocated to strata approximately in proportion to the area of each stratum with specific assignment within strata on a random basis. A 30-min tow at an average speed of 3.5 knots (6.5 km/h) is made at each station. The total catch from each tow is sorted to species and the number, weight, and length frequency determined and recorded. Samples are collected for shoreside processing.

Relative abundance indices for Georges Bank haddock (*Melanogrammus aeglefinus*) and yellowtail flounder (*Limanda ferruginea*) were based on strata 13–25 of the standardized trawl survey. The Southern New England yellowtail flounder relative abundance index was based on strata 1–12 and the haddock index for statistical area 4X of the Northwest Atlantic Fisheries Organization (NAFO SA 4X) was based on strata 31–34.

Autumn surveys are more representative of population size approximately 2 mo later, at the beginning of the next year of the survey. Therefore, the survey index for fish age $a-1$ from the autumn of year $t-1$ is used as a relative abundance index for fish age a in year t. For both species, 1-yr-old fish (during autumn surveys) are considered as pre-recruits which recruit to the fishery during the following year.

Commercial catch data used in this study are from statistical bulletins of the Northwest Atlantic Fisheries Organization

and various unpublished stock assessment documents. For yellowtail flounder the annual catch was calculated for the year beginning October 1 so as to be in phase with autumn surveys. For haddock, the available compilation of data made it more convenient to use catch on a calendar year basis. Following Brown and Hennemuth (1971), Lux (1969), and Clark et al. (1982), natural mortality of both species was assumed to be 0.2.

Analytical Method

Non-Age-Structured Model

The first-order difference equation,

$$(1) \quad N(t+1) = [N(t) - C(t) + R(t)] \exp(-M),$$

relates the population size in numbers for a given year, $N(t+1)$, to population size in the preceding year, $N(t)$, minus the catch, $C(t)$, plus recruitment, $R(t)$, all discounted by natural mortality, M. The model implicitly assumes that the fish stock is closed to migration. Natural mortality is assumed to occur at a constant rate, independently of age and year. More detailed information about natural mortality could easily be incorporated into the model but such information must come from an independent source.

Equation 1 is approximate since it assumes that catch occurs instantaneously at the beginning of a time interval of 1 yr and that natural mortality occurs continuously. To test whether this approximation is adequate in our case we used an alternate form of Equation 1 in which the year is partitioned into four quarters. Thus catch is applied quarterly, although within each quarter, the same assumptions are applied as in Equation 1. Even greater resolution can be achieved by dividing the year into smaller intervals.

The survey relative abundance, $n(t)$, is related to the absolute population size by a catchability coefficient, q, such that

$$(2) \quad n(t) = qN(t)$$

and assuming the pre-recruits have the same catchability,

$$(3) \quad r(t) = qR(t).$$

As noted previously, $n(t)$ is the stratified mean catch per tow of recruited age fish from the autumn trawl survey of year $t-1$. The recruitment index is based on survey catch of pre-recruits. Substituting for $N(t)$ and $R(t)$ in the dynamic equation and multiplying by q, we obtain the regression equation:

$$(4) \quad n(t+1) = [n(t) - qC(t) + r(t)] \exp(-M) + \epsilon(t); \quad (t=1, i-1)$$

where $\epsilon(t)$ is the equation error or natural variability not accounted for by the dynamic model. Stated as such, the problem is a standard linear least-squares estimation of q. If M is unknown, it can also be estimated, but the estimates of M and q are highly correlated and therefore subject to considerable error.

The new twist to the problem is that both $n(t)$ and $r(t)$ have associated measurement errors. Following Clark and Brown's (1977) justification for a logarithmic transformation of the survey data, observation error is assumed to be a lognormally distributed random variable with mean one. This makes intuitive sense in that changes in trawl efficiency ought to have a multiplicative effect on the catch and it also insures against negative population estimates. The four populations considered here have declined markedly during the years for which we have data. Logarithmic transformation tends to equalize the weights given to high and low abundance indices in the fitting procedure.

The measured relative abundance, $\tilde{n}(t)$, is related to the "true" relative abundance by

$$(5) \quad \tilde{n}(t) = n(t) \exp[\eta(t)]; \ (t=1, i).$$

Similarly, for the recruits,

$$(6) \quad \tilde{r}(t) = r(t) \exp[\delta(t)]; \ (t=1, i-1)$$

where $\eta(t)$ and $\delta(t)$ are normally distributed random variables.

Errors associated with the catch measurements are not considered for two reasons. Firstly, these errors, which include misreporting and nonreporting of the commercial catch and discards, are probably more systematic than random in nature. In other words, catch may have been consistently underestimated. Secondly, the correlation between the estimators of $C(t)$ and q precludes reliable estimation of both.

Given a time series of i years of data, there are i expressions for Equation 5 and $i-1$ expressions for Equations 4 and 6. This gives $m = 3i - 2$ residual errors with $p = 2i$ parameters to be fitted and $m - p = i-2$ degrees of freedom.

Age-Structured Model

The age-structured model is similar to the non-age-structured model except that both the survey relative abundance and the commercial catch are divided by age-class. In lieu of Equation 1, we write

$$(7) \quad N(t+1, a+1) = [N(t,a) - C(t,a)] \exp(-M).$$

Assuming the catchability coefficient to be constant over all age-classes,

$$(8) \quad n(t,a) = qN(t,a).$$

Here $n(t,a)$ is the stratified mean catch per tow of age $a-1$ fish from the autumn trawl survey of year $t-1$.

In practice, because there are so few survivors in the terminal age-classes, it is convenient to lump them into a "plus" group (e.g. for haddock our plus group is age 9 and older fish). Since fish can remain in the plus group for more than 1 yr, we need two forms of Equation 4 for the age-structured model. If j is the plus group (in this case 9+) the dynamic equation for ages 1 to $j-1$ is

$$(9a) \quad n(t+1, a+1) = [n(t,a) - qC(t,a)] \exp(-M) + \epsilon(t,a); \quad (t=1, i-1; a=1, j-2)$$

and for the plus group, age j

$$(9b)\quad n(t+1,j) = [n(t,j) + n(t,j-1) - qC(t,j) - qC(t,j-1)]\exp(-M) + \epsilon(t,j-1); \quad (t = 1, i-1)$$

Again, the measured relative abundance $\tilde{n}(t,a)$ is related to the "true" relative abundance by

$$(10)\quad \tilde{n}(t,a) = n(t,a)\exp[\eta(t,a)];\ (t = 1, i;\ a = 1, j)$$

Given data for i years and j age-classes we have $(i-1)\cdot(j-1)$ expressions for Equations 9a and b and $i\cdot j-1$ expressions for Equation 10. There is no expression for $n(i,1)$ because it is not included in either of the dynamic Equations 9a or b. This gives a total of $m = i\cdot j-1 + (i-1)\cdot(j-1)$ residual errors with $p = i\cdot j$ parameters to be fitted and $m - p = (i-1)\cdot(j-1) - 1$ degrees of freedom.

Parameter Estimation

The parameters of the regression models were estimated by fitting Equations 4–6 or 9–10 simultaneously by least-squares methods. For the non-age-structured model the sum of squares is

$$(11)\quad SS(\underline{\theta}) = \sum_{t=1}^{i-1}(\epsilon_t)^2 + \sum_{t=1}^{i}(\eta_t)^2 + \sum_{t=1}^{i-1}(\delta_t)^2.$$

The error terms, ϵ_t, η_t, δ_t, are from Equations 4, 5, 6, respectively. The vector of parameters to be estimated is $\underline{\theta}' = [q, n(1), \ldots, n(i), r(1), \ldots, r(i-1)]$.

The equivalent expression for the age-structured model is

$$(12)\quad SS(\underline{\theta}) = \sum_{t=1}^{i-1}\sum_{a=1}^{j-1}(\epsilon_{t,a})^2 + \sum_{t=1}^{i}\sum_{a=1}^{j}(\eta_{t,a})^2$$

where the error terms, $\epsilon_{t,a}$, $\eta_{t,a}$, are from Equations 9 and 10, respectively. In this case the parameters to be estimated are $\underline{\theta}' = [q, (n(t,a)$ for $t = 1,i$ and $a = 1,j)]$.

The sets of equations, 4–6 or 9–10, are nonlinear in the parameters to be estimated; therefore nonlinear regression must be used. There are several methods for computing nonlinear least-squares estimators (Draper and Smith 1966; Gallant 1975), and a program implementing one of these methods is available in most statistical program libraries.

We used the nonlinear regression subroutine, ZXSSQ, from the International Mathematical and Statistical Library on the WHOI VAX 11/780 computer. ZXSSQ is a finite-difference, Levenberg–Marquardt routine for solving nonlinear least-squares problems. Due to the difference in magnitude between survey and commercial catches, q was multiplied by 10^6 for numerical efficiency of the algorithm.

In Equations 11 and 12 it is implicitly assumed that the equation and measurement error terms have equal variance. This is assumed because we do not know the actual variance associated with each type of error. We examined the importance of this assumption by applying a weighting factor to the error terms and examining the sensitivity of the parameter estimates. Using the non-age-structured model, for example, we denote the sums of squares SS_ϵ, SS_η, and SS_δ for the respective error terms. Equation 11 can then be rewritten as

$$(13)\quad SS(\underline{\theta}) = SS_\epsilon + w^2(SS_\eta + SS_\delta).$$

Equal weight was given to the measurement errors for pre-recruits and recruited fish because the two indices come from the same survey. The weighting factor, w, was varied over five orders of magnitude to examine the importance of the assumption of equal variances.

Confidence Intervals

Two methods are used to calculate confidence intervals for the parameter estimates. The first method is based on the asymptotic normality of the least-squares estimator. The subroutine, ZXSSQ, returns the approximate Jacobian, $J(m\times p)$, evaluated at the least-squares estimator $\hat{\underline{\theta}}$. The variance-covariance matrix, $C(p\times p)$, is then

$$(14)\quad C = (J'J)^{-1}\, SS(\hat{\underline{\theta}})/(m - p).$$

A $1-\alpha$ confidence interval may be found for any parameter $\hat{\theta}_k$ from the α-critical value of the t-variate with $m - p$ degrees of freedom, as

$$(15)\quad \hat{\theta}_k \pm t_\alpha \sqrt{c_{kk}}$$

where c_{kk} denotes the kth diagonal element of matrix C.

The second method is based on the likelihood ratio test. This method involves fixing the parameter of interest ($\theta_k = \theta_{ko}$) and calculating the constrained minimum sum of squares, $SS(\underline{\theta}\,|\,\theta_k = \theta_{ko})$ with subroutine ZXSSQ. The $1-\alpha$ confidence limits are then given by values of θ_{ko} which satisfy

$$(16)\quad [SS(\underline{\theta}\,|\,\theta_k = \theta_{ko}) - SS(\hat{\underline{\theta}})]/SS(\hat{\underline{\theta}}) = F_\alpha$$

where F_α is the α-critical level of the F-distribution with 1 numerator and $m - p$ denominator degrees of freedom.

A succession of least-squares fits must be carried out until the critical values of θ_{ko} are found. Gallant (1975) found a slight sacrifice in power for the computational convenience of the first method.

Results

The non-age-structured model was fit for yellowtail flounder (Georges Bank and Southern New England populations) and haddock (Georges Bank). The age-structured model was fit for haddock (Georges Bank and NAFO SA 4X populations). Both versions of the model were applied to Georges Bank haddock, thus allowing the performance of the two forms of the model to be compared. For yellowtail flounder the model was fit with catch reported both in-phase (October–September) and out-of-phase (calendar year). There was little difference in parameter estimates, thus demonstrating that estimates are not sensitive to lagging of the catch, at least for fisheries with a seasonal distribution similar to yellowtail (relatively uniform throughout the year). Only

TABLE 1. Estimated catchability coefficients. Method 1 for estimating confidence intervals is based on the asymptotic normality of the least-squares estimator (Equation 15); method 2 is the likelihood ratio test (Equation 16). See text for more detailed explanation.

Population	Model	Catchability coefficient[a]	95% confidence interval	
			Method 1	Method 2
Yellowtail flounder (SNE)[b]	non-age-structured	0.313	0.189−0.437	0.284−0.465
Yellowtail flounder (GB)	non-age-structured	0.107	0.061−0.153	0.065−0.160
Haddock (GB)	non-age-structured	0.257	0.149−0.365	0.164−0.384
Haddock (GB)	age-structured	0.238	0.194−0.282	0.198−0.283
Haddock (4X)	age-structured	0.340	0.265−0.417	0.261−0.425

[a]All catchability coefficients and associated confidence intervals have been multiplied by 10^6.
[b]SNE = Southern New England; GB = Georges Bank; 4X = NAFO Statistical Area 4X.

results based on in-phase catch are reported for yellowtail flounder.

Estimates of q and associated confidence intervals are given in Table 1. The catchability coefficients agree quite closely with previous estimates by Clark and Brown (1977) even though their coefficients are based on weight rather than numbers. Confidence intervals calculated by the two different methods are approximately the same length, although intervals calculated by method 2 are shifted toward slightly higher values. Very similar estimates of q for Georges Bank haddock are obtained from the non-age-structured and age-structured models. The confidence intervals, however, are considerably narrower for the age-structured model.

The catchability coefficient is the product of gear efficiency (i.e. proportion of the fish in the path of the gear that are captured), and the ratio of the area sampled by a standard tow to the total area surveyed. Since the area sampled is standardized, gear efficiency between areas can be computed by normalizing to the area surveyed. In the case of Southern New England (strata 1−12) and Georges Bank (strata 13−25), the survey areas are almost identical. Therefore relative gear efficiency is indicated by estimates of q.

Differences in gear efficiency (as indicated by catchability coefficients) within species but between areas probably reflect differences in bottom topography. For yellowtail flounder, the catchability coefficient for the rougher bottom of Georges Bank ($q = 0.107 \times 10^{-6}$) would be expected to be lower than for Southern New England ($q = 0.313 \times 10^{-6}$).

The difference in catchability between Georges Bank yellowtail ($q = 0.107 \times 10^{-6}$) and haddock ($q = 0.257 \times 10^{-6}$) could reflect their different life habits. One might speculate that the yellowtail's habit of lying on the bottom makes it less prone to being caught by the otter trawl. In fact, the NEFC otter trawl survey is an outgrowth of earlier Georges Bank haddock surveys. Thus, the survey would be expected to be particularly efficient for this population.

Yellowtail flounder is an excellent candidate for application of our approach because, although total catch has been reported, age composition suitable for VPA is not now available. Therefore, a new method, such as the one applied here, is necessary. Furthermore, although trawl surveys track trends in abundance, individual surveys sometimes appear anomalous. The statistical method used here is amenable to this situation. The results are shown in Fig. 2 and 3. Note in Fig. 2 how the fitting procedure smooths the survey abundance and appears to distinguish between true fluctuation and measurement error. In 1966, for example, the low abundance of age 2 and older (2+) fish and the low level of 1-yr-olds in the previous year is consistent with the model. On the other hand, the peak in 2+ fish in 1972 is inconsistent with the model because recruitment was falling in the preceding years.

The non-age-structured model was also fit for yellowtail flounder with catch applied on a quarterly basis. Natural mortality was still applied continuously, but quarterly catches were applied as they were actually reported. The results indicate the sensitivity of Equation 1 to the implicit assumption that all catch is taken at the beginning of the year. Estimates of q based on catch applied quarterly are lower than those based on Equation 1, but not substantially so (5% lower for Southern New England and 10% lower for Georges Bank).

Southern New England yellowtail flounder data were also used to examine the effect of differential weighting of the sums of squares. The weighting factor, w, of Equation 13 was varied over five orders of magnitude (from 0.01 to 100) and the parameter estimates compared (Table 2). There is no apparent trend in q-estimates for different weighting factors. Relative abundance estimates for the different weights are not shown but only in the extreme cases ($w = 0.01$ and $w = 100$) were the abundance estimates substantially different than those for $w = 1.0$. Although we do not know the correct value of the weighting factor, it is most likely to be within the range 0.1 to 10. In all other trials reported in this paper we used $w = 1.0$.

TABLE 2. Results of weighted least squares for Southern New England yellowtail flounder.

w	q	% difference from $w = 1$
0.01	0.342×10^{-6}	9.3
0.1	0.278×10^{-6}	−11.1
1.0	0.313×10^{-6}	0.0
10	0.322×10^{-6}	2.9
100	0.307×10^{-6}	−1.9

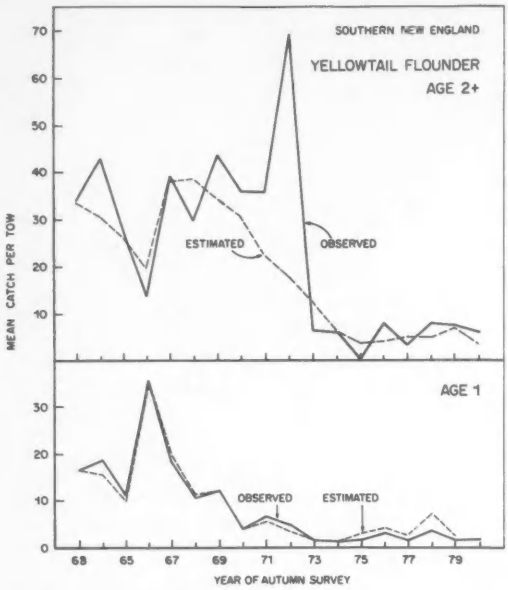

FIG. 2. Observed (solid line) against estimated (dashed) abundance for Southern New England yellowtail flounder.

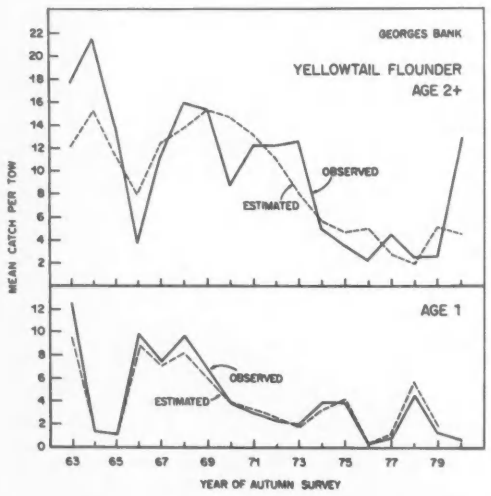

FIG. 3. Observed (solid line) against estimated (dashed) abundance for Georges Bank yellowtail flounder.

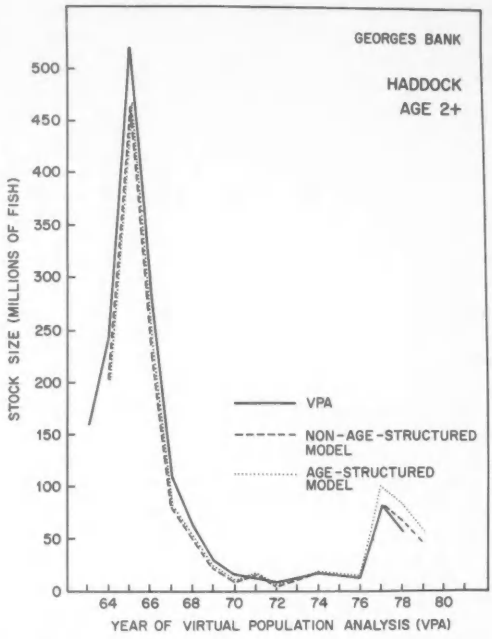

FIG. 4. Population size of Georges Bank, age 2+ haddock as estimated by virtual population analysis (solid line), non-age-structured model (dashed line) and age-structured model (dotted line). The VPA estimates are from Clark et al. (1982).

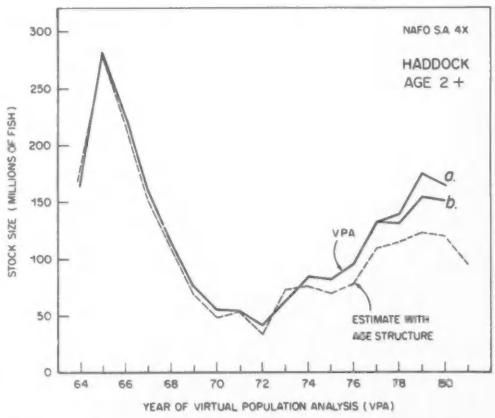

FIG. 5. Population size of NAFO SA 4X, age 2+ haddock as estimated by VPA (solid line) and age-structured model (dashed line). The VPA estimates are from O'Boyle (1981). The labels "a" and "b" refer to the two different methods used to initialize the VPA.

Haddock was considered in order to allow a comparison between population estimates generated by the method presented herein and those obtained by VPA. Age 2+ population estimates were generated by dividing the smoothed survey abundance by the appropriate catchability coefficients. Let $N(t)$ be the age 2+ population size in year t. For the age-

grouped model, $N(t)$ is estimated by $[\hat{r}(t) + \hat{n}(t)]/\hat{q}$; for the age-structured model, $N(t)$ is estimated by $\sum_{a=2}^{j} \hat{n}(t,a)/\hat{q}$. The results are shown in Fig. 4 and 5. Not only do our two models give similar estimates of q for Georges Bank, but it can be seen in Fig. 4 that, except for the final 3 yr, the population estimates are almost indistinguishable.

In both areas (Georges Bank and NAFO SA 4X) there is close agreement between the alternate estimates of haddock population size. It should be noted that the VPA estimates for the final few years are sensitive to the fishing mortality estimates used to initiate the analysis. These most current estimates are therefore the most prone to error. O'Boyle (1981) used two different approaches to initialize his VPA for 4X haddock. The sensitivity of the results for the most recent years is demonstrated in Fig. 5.

The disparity between our method and VPA for Georges Bank haddock is greatest for the mid-1960s and late 1970s. During the former, our estimates are lower than VPA estimates. VPA would overestimate actual population size if the catch was overestimated. In fact, most of the catch during the mid-1960s was by distant-water fishing vessels (e.g. USSR) which only reported their catch in weights, not numbers. The number caught had to be estimated by assuming that the length composition was comparable to the length composition of the research vessel trawl survey catch (Clark et al. 1982). Thus, VPA results for the brief period when the distant-water fleets dominated the fishery are particularly uncertain.

Similarly, the disparity between our method and VPA during the late 1970s may reflect bias in the VPA. During the late 1970s catch quotas were extremely restrictive; therefore an unknown amount of the actual catch was unreported, discarded, or misreported as being from SA 4X (S. H. Clark, personal communication). Thus, the VPA for Georges Bank haddock probably underestimates population size during the late 1970s. Furthermore, if some Georges Bank catch was misreported as SA 4X catch, then the VPA for the latter would overestimate population size. This may explain the disparity between our method and VPA for the mid- and late 1970s (Fig. 5). Population size indices during this period (VPA estimates) are higher than those based on our method.

The relatively large confidence interval about the estimates of q for 4X haddock reflects the high variability of the survey data for that area. The trawl survey sample size for strata within SA 4X is relatively small.

Discussion

We have described and applied a new method of estimating population size based on relative abundance indices. In addition to estimating catchability coefficients, the technique smooths the survey data. Using our method, population size estimates for haddock compare favorably with VPA estimates.

The Georges Bank haddock applications show that the non-age-structured and age-structured models yield virtually identical population size estimates. This supports application of the non-age-structured model for estimating the size of populations, such as yellowtail flounder, where the age composition of the catch is unknown. Where commercial catch-at-age data are available, there are two advantages to using the age-structured model over the non-age-structured. Firstly, the age-structured model provides smoothed population estimates by age. These values might be used for catch-curve analysis to estimate total mortality rate. Secondly, the confidence intervals about the parameters estimated by the age-structured model are smaller because this model has more degrees of freedom.

The similarity between our estimates of population size and the VPA estimates is perhaps not surprising since both procedures are based on the same catch history and both make the same assumptions about natural mortality. However, an important difference between our age-structured model and VPA should be pointed out. The system of equations for VPA is underdetermined (Pope 1979) and therefore assumptions must be made about the fishing mortalities acting on the oldest age of each year class. In general, it is the estimates for the final few years of the analysis which are most sensitive to the starting fishing mortalities. By using the survey data as independent measures of population abundance, our method avoids the problem of an underdetermined system.

Doubleday (1981) presents a method for efficient estimation of the terminal fishing mortality rate necessary to initiate sequential population analyses (e.g. VPA). Research vessel abundance indices, by age, are used iteratively to calibrate survivor estimates. The catchability coefficient is allowed to vary with age.

Gray (1979) used catch-per-unit-effort at age to substitute for numbers at age in a manner somewhat analogous to our use of relative abundance indices. Where survey data are available as independent measures of relative abundance, our method is preferable because catch-per-unit-effort is not independent of the commercial catch.

The validity of population size and parameter estimates derived here depends on several assumptions; these are discussed below.

The assumption that catch occurs instantaneously at the beginning of a year affects estimates of q. If catch is distributed over the year, then average population size is higher, and more natural deaths occur. Thus, fewer fish need to be caught to account for the differences between $n(t)$ and $n(t+1)$ and therefore q is overestimated.

The results, for yellowtail flounder, when catch was applied quarterly, confirm that the assumption of total annual catch at the beginning of the year causes a positive bias of q, but only by 5 or 10% in this case. Even greater accuracy could be achieved by dividing a year into shorter intervals. The limit of accuracy is determined by the interval of catch reporting.

Alternatively, total annual catch may be assumed to occur instantaneously at any point, t_c, during the year. Then,

$$(17)\quad N(t+1) = [N(t) + R(t)]\exp(-M) - C(t)\exp[-M(1 - t_c)]$$

is substituted for Equation (1) where $0 \leq t_c < 1$. Pope (1972) used a form analogous to Equation 17, with $t_c = 0.5$, in order to investigate the accuracy of virtual population analysis. If catch is distributed relatively evenly throughout the year, then $t_c = 0.5$ is probably adequate.

Although the selectivity of the otter trawl is not known,

there are probably age-specific differences in catchability coefficients, especially for young fish. It is not possible to estimate a separate q for each age-class because of the way in which the regression model is formulated. One approach would be to fit a catchability coefficient for sequential pairs of age-classes. This approach, however, would lack the continuity provided by the dynamic equations and the estimates of q would therefore be less certain. The catchability coefficients calculated by our method may be considered in a sense as weighted means of age-specific qs. If so, the estimates of population by age will be biased but the total population estimates should be unbiased.

It can be seen from Equations 4 and 9 that estimates of q are sensitive to the value of M, the natural mortality. If $M > 0.2$ then q has been overestimated and vice versa. Due to the high correlation between estimates of q and M, M cannot be reliably estimated by this method. Using an analogy with analysis of variance, Pope (1979) explained why catch-at-age data contain little information on the level of natural mortality.

Natural mortality is probably higher during the first few years of life. In addition to natural mortality, young fish are also subject to the mortality resulting from unreported discarding of large numbers of 1- and 2-yr-olds (Clark et al. 1982). If the catchability of young fish is lower than for adults, but the natural mortality rate is higher, then, at least for the purpose of estimating q, these two biases should tend to cancel out.

The relative weights assigned to each of the error terms affects the values of the parameter estimates. In our example with yellowtail flounder this effect was rather small except for extreme values of the weighting factors. It would be most desirable to have an independent estimate of the ratio of error variances so that the sums of squares could be weighted accordingly.

The measurement error variance can be at least partially accounted for using the within-survey variance of mean catch per tow. This gives only the component of variance due to the spatial distribution of the fish during a specific survey; there is another, unknown, component of measurement-error variance due to environmental effects on the distribution of the fish and trawl efficiency. Thus, under different environmental conditions, the results of a survey would have been different, even with the same size fish population. This environmental variability (1972 for Southern New England yellowtail flounder is probably an example of it) is not included in the variance estimate for a survey mean (Byrne et al. 1981). Even if we neglect the environmental component of measurement-error variance, we need to know the equation-error variance in order to properly weight the sums of squares.

The predictive value of this method is limited by the fact that the recruits for the final year of the analysis do not enter into the dynamic equation. Therefore, it is not possible to take account of measurement error. Using the non-age-structured model, for example, if i is the last year of the time series for which there is data, the abundance in the following year, $n(i+1)$, can be predicted by prescribing the catch, $C(i+1)$. The estimates of $n(i+1)$, however, must be based on the observed recruitment, $\bar{r}(i)$, since $r(i)$ is not included in the dynamic equation (4). Similarly, for the age-structured model, the population estimate for year $i+1$ will include the error in measuring recruitment in year i.

The reliability of the estimation procedure could be tested on simulated data sets for which the true abundance is known. Simulated data sets could be created by the addition of error terms of a prescribed distribution to a time series of abundance generated by the dynamic model. The fitting technique could then be tested for reconvergence about the simulated abundance indices.

We have demonstrated a method for estimating population size by simultaneously estimating the catchability coefficient of a standardized index of abundance and smoothing the annual values of the index. The method is based on several assumptions, yet it is flexible enough for application to many problems.

Acknowledgments

W. K. Smith was instrumental in selection of the statistical method used in this paper. D. Ludwig, J. Beddington, and J. Pope provided helpful comments on an earlier report on this work. J. Collie was supported by the W.H.O.I. Education Office.

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Influence of Hatchery Smolt Releases on Adult Salmon Production and its Variability

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McCarl, B. A., and R. B. Rettig. 1983. Influence of hatchery smolt releases on adult salmon production and its variability. Can. J. Fish. Aquat. Sci. 40: 1880–1886.

Regression studies of salmon stock-recruitment relations require a priori assumptions concerning the nature of stock variability as influenced by smolt populations. Such assumptions can lead to biased estimates of the relationships of smolts to the production of adult salmon. This paper utilizes a statistical method which allows the data to determine the interrelationship of smolts and adult production mean and variability without imposing a priori restrictions on the form of such. The estimation process yields two estimated relationships — one explaining the effect of hatchery releases on expected adult production and another explaining the effects of the hatchery releases on the standard deviation of adult production. Application of this model suggests that the standard deviation of adult production increases with the square of the number of seaward migrants both for Hokkaido chum salmon (*Oncorhynchus keta*) and for Oregon coho salmon (*O. kisutch*) and that incorrect inferences may have been obtained about density dependence by other authors because of the imposed a priori assumptions and/or data adequacy.

McCarl, B. A., and R. B. Rettig. 1983. Influence of hatchery smolt releases on adult salmon production and its variability. Can. J. Fish. Aquat. Sci. 40: 1880–1886.

Les études de régression des relations stock-recrutement du saumon reposent sur des hypothèses *a priori* concernant la nature de la variabilité des stocks, telle qu'influencée par les populations de smolts. Il y a danger que de telles hypothèses conduisent à des estimations biaisées des relations smolts-production de saumons adultes. L'étude décrite dans le présent article fait appel à une méthode statistique grâce à laquelle les données peuvent servir à déterminer la relation entre smolts et moyenne de la production d'adultes et sa variabilité, sans imposer de restrictions *a priori* sur la forme de cette relation. On obtient ainsi deux relations estimées : l'une expliquant l'effet des peuplements de poissons d'élevage sur la production d'adultes et l'autre expliquant l'effet des peuplements sur l'écart type de cette production. L'application de ce modèle donne à penser que l'écart type de la production d'adultes augmente en fonction du carré du nombre de poissons se dirigeants vers la mer, tant pour le saumon keta (*Oncorhynchus keta*) de Hokkaidō que pour le saumon coho (*O. kisutch*) de l'Orégon. Il suggère également que les déductions d'autres auteurs ont pu être incorrectes à cause des hypothèses imposées *a priori* et (ou) la pertinence des données.

Received December 15, 1982
Accepted July 12, 1983

Reçu le 15 décembre 1982
Accepté le 12 juillet 1983

Efforts to enhance salmonid stocks are and have been characterized by considerable variability in their consequences. Although variability is a natural phenomenon in all fisheries, enhancement programs may be influencing the level of variability observed. This possibility has led to suggestions (such as that in Walters [1975]) that managers include variability factors in the design of fishery management strategies. Such a procedure would require information about the amount of production variability which should be attributed to the strategies.

Recently the influence of variability on the estimation of adult salmon production has been examined. Peterman (1981, p. 1113) argued that the form of the variability as assumed in an estimation effort "can determine the shape of a curve fit." Peterman (1981, p. 1114) goes on to argue that a multiplicative log normal error term should be used in equations for estimating adult production instead of an additive error term because of (a) theoretical arguments regarding the interrelationship of fish abundance and mortality agents and (b) empirical observations. However, Peterman's analysis does not develop any estimate on the form of variability and, as will be shown below, makes important a priori assumptions regarding the exact form of variability.

The primary purpose of this paper is to utilize a statistical method, due to Just and Pope (1978, 1979), in a fisheries context which allows one to develop estimates of how variability is influenced by enhancement efforts. In the process of this application several other results emerge. First we will demonstrate, following and extending Peterman (1981), the

Printed in Canada (J7175)
Imprimé au Canada (J7175)

implicit assumption regarding the additive and log normal error terms in regression estimation and we will show that the Just–Pope method operates under much less restrictive assumptions which we will illustrate are important in a fisheries context. Second we will develop estimates of the consequences of hatchery releases on adult salmonid production variability for the Oregon coho (*Oncorhynchus kisutch*) and Hokkaido chum (*O. keta*) fisheries. Third we will comment on implications for fisheries management within the context of the data sets used.

Before presenting the research methods, we need to qualify our analysis. The empirical work reported here aggregates smolts and adults from a number of rather diverse salmon stocks. This degree of aggregation could be subject to a number of difficulties. Smolt-to-adult relationships can vary greatly over time and space due to variation in hatchery conditions such as disease, feeding rations, pond loading densities, time of release, genetic diversity, quality control operations, ratio of hatchery to wild production, and freshwater environmental conditions (for example, see the list in Oregon Department of Fish and Wildlife, 1982). We have three reasons for treating data at such a high level of aggregation and ignoring such important variables. First, aggregate smolt-to-adult relationships have been widely studied by fishery scientists (see the review in Peterman (1981)) and we are attempting to generalize this work. Second, public debate has, in cases, revolved around these aggregate numbers and resolution of issues regarding them is potentially valuable in public policy formation. For example, in Oregon the optimum number of hatchery coho smolt releases is discussed in aggregate even though analytical problems, including several discussed in this paper, do not permit a single numerical goal to be specified at this time (Oregon Department of Fish and Wildlife 1982, p. II.E-1). Third, we were attempting to demonstrate an alternative, less restrictive, estimation method and it seemed desirable to use data arising from fishery settings which were consistent with previous efforts (Peterman 1981).

Methods

The proper form of the error term has long been a concern in regression analysis as manifest in the concern with heteroscedasticity (see Judge et al. (1980) or Kmenta (1971)). Peterman (1981) discussed this problem in a fisheries setting and conducted analysis designed to discover the appropriate form for random variability considering two alternate models:

$$(1)\quad A_1 = C_1 S^{k_1} + V_1$$

$$(2)\quad A_2 = C_2 S^{k_2} \exp(V_2)$$

where

A_i = adult production as predicted by model i,
S = number of smolts (or fry for chums),
C_i = survival rate parameter in model i,
k_i = parameter indicating degree of density dependence in model i, and
V_i = error term which is normally distributed and additive in model $i = 1$ or multiplicative in model $i = 2$.

Peterman's analysis leads to the conclusion that the second model should be used because of the interrelationships of S and variability. However, following Just and Pope (1978, 1979), it can be argued that the two models embody very restrictive assumptions in terms of variability and that a much more general specification is possible. This may be shown as follows:

The mean of model 1 is found by taking the expectation of the production level (A_1)

$$E(A_1) = E(C_1 S^{k_1} + V_1) = C_1 S^{k_1} + E(V_1) = C_1 S^{k_1}$$

since the term $C_1 S^{k_1}$ is a constant and the expected value of the error term equals zero. Thus the mean response in model 1 given any release policy S is simply that given by the regression equation. The variance of adult production model 1 equals

$$\begin{aligned}\mathrm{Var}(A_1) &= E(A_1 - E(A_1))^2 \\ &= E(C_1 S^{k_1} + V_1 - C_1 S^{k_1} - E(V_1))^2 \\ &= E(V_1 - E(V_1))^2 = \mathrm{Var}(V_1) \text{ by definition}\end{aligned}$$

Thus the variability around the mean in model 1 is a constant independent of the number of smolts as asserted in Peterman.

The mean of model 2 is

$$\begin{aligned}E(A_2) &= E(C_2 S^{k_2} \exp(V_2)) \\ &= C_2 S^{k_2} E(\exp(V_2)) = C_2 S^{k_2} \mu_2\end{aligned}$$

since $C_2 S^{k_2}$ is a constant and μ_2 is defined as the mean of the exponential function of V_2. Thus the mean response within model 2 given a smolt release policy is simply that given by the equation times a constant which is the expectation of the exponential error term.

The variance of model 2 is

$$\begin{aligned}\mathrm{Var}(A_2) &= E(C_2 S^{k_2} \exp(V_2) - C_2 A^{k_2} \mu_2)^2 \\ &= (C_2 S^{k_2})^2 \mathrm{Var}(\exp(V_2)) \\ &= \frac{[E(A_2)]^2 \mathrm{Var}(\exp(V_2))}{\mu_2^2} \\ &= [E(A_2) CV(\exp(V_2))]^2\end{aligned}$$

where $\mathrm{Var}(\exp(V_2))$ is the variance of the exponential function of V_2 and $CV(\exp(V_2))$ is the coefficient of variation of the exponential function of V_2. Thus within model 2 (the multiplicative error term specification) the variance of adult production is a constant times the square of the mean of adult production. The marginal effect on expected production and variance can also be derived. These estimates result in

$$\frac{dE(A_2)}{dS} = k_2 \frac{E(A_2)}{S}$$

and

$$\begin{aligned}\frac{dV(A_2)}{dS} &= 2[CV(\exp(V_2))]^2 E(A_2) \frac{dE(A_2)}{dS} \\ &= \frac{2[CV(\exp CV_2))]^2 k_2 E[A_2]^2}{S}\end{aligned}$$

Assuming that k_2 is positive (which assumes that greater smolt releases increase adult production to some degree) then this illustrates Peterman's assertion (1981, p. 1113) that the

random process (in model 2) exhibits "higher absolute variation in total adult returns as abundance increases." However, the equations also show that both the mean and variance of adult production due to changes in the number of smolts released will vary directly in proportion to k_2 with the same sign as k_2.

While these demonstrations simply illustrate Peterman's assertions, there is a rather troubling aspect to them. Namely, the data have nothing to do with the form of the variability exhibited by the functions chosen by Peterman. His choice of functional form requires the variance to be either constant or a constant times the square of the mean. There is no room for decreasing or constant variability in the second function unless the average productivity function exhibits declining or constant productivity simultaneously.

Further, the restriction on variance in Peterman's preferred multiplicative model has broader implications. Peterman (1981, p. 1118) suggests that there are certain factors which may cause variability to decrease, for example, "Larger body size at release. . . should produce lower variability in adult returns. . . ." Expanding function 2 so that we have as a second explanatory factor body size (B), we get

$$(2a) \quad A_3 = C_3 S^{k_3} B^{d_3} \exp(V_3).$$

The mean for this function is

$$E(A_3) = C_3 S^{k_3} B^{d_3} E(\exp(V_2))$$

The instantaneous rates of change in expected adult production with respect to smolts and body size are

$$\frac{\partial E(A_3)}{\partial S} = \frac{k_3 E(A_3)}{S} \text{ and } \frac{\partial E(A_3)}{\partial B} = \frac{d_3 E(A_3)}{B}$$

The variance for this function is

$$\begin{aligned} \mathrm{Var}(A_3) &= (C_3 S^{k_3} B^{d_3})^2 \ \mathrm{Var}(\exp(V_3)) \\ &= [E(A_3) CV(\exp(V_3))]^2 \end{aligned}$$

and the instantaneous rates of change in variance of adult production with respect to smolts and body size are

$$\begin{aligned} \frac{\partial \mathrm{Var}(A_3)}{\partial S} &= \frac{2k_3 \mathrm{Var}(A_3)}{S} \\ &= 2\, E(A_3)[CV(\exp(V_3))]^2 \frac{\partial E(A_3)}{\partial S} \end{aligned}$$

and

$$\begin{aligned} \frac{\partial Var(A_3)}{\partial B} &= \frac{2d_3 \mathrm{Var}(A_3)}{B} \\ &= 2\, E(A_3)\,[CV(\exp(V_3))]^2 \frac{\partial E(A_3)}{\partial B} \end{aligned}$$

This relationship (i.e. the form of equation 2a) does not permit larger body size at release to both give higher yields (which would imply $d_3 \geq 0$ in $\partial E(A_3)/\partial B$) and produce lower variability (which would imply $d_3 \leq 0$ in $\partial V(A_3)/\partial B$).

Conceptually, it appears important to allow the data to specify the exact form of variability and in turn, to provide a basis for testing hypotheses such as those mentioned in Peterman (1981). A desire to do this calls for the use of a different functional form which does not impose a priori restrictions on variability. Such a form was developed by Just and Pope.

The Just–Pope Production Function

Just and Pope (1978, 1979) suggest a function of the following form which possesses flexible properties with respect to estimation in the context of variability:

$$Y = f(x) + h^{\frac{1}{2}}(X) \exp(V)$$

where

Y = yield (i.e. A above)
X = vector of nonstochastic inputs (i.e. S, B above), and
V = normally distributed multiplicative error term.

They demonstrate that

$$E(Y) = f(X)\, E(\exp(V))$$

and

$$\mathrm{Var}(Y) = h(X)\, \mathrm{Var}(\exp(V)).$$

Thus $f(X)$ is an estimate of the mean response of production due to X and $h^{\frac{1}{2}}(X)$ is an estimate of the component of the standard deviation of production due to X_n. Particularizing this to the fisheries example above, the following model could be specified. Let

$$f(X) = C_4 S^{k_4} B^{d_4}$$

and

$$h^{\frac{1}{2}}(X) = C_5 S^{k_5} B^{d_5}.$$

This form permits flexible estimation of the relationship of the input parameters to both the mean and the standard error of adult production. For example, if $k_4 \geq 0$ and $k_5 \geq 0$, one obtains a form similar to the Peterman multiplicative case where both the mean and standard error of adult production increase with smolts (without the restriction that the variance increases with the square of the mean), while the case where $d_4 \geq 0$ and $d_5 \leq 0$ corresponds to Peterman's body size hypothesis. In the process of estimation (discussed below) one obtains parameter estimates and standard errors for the C's, k's, and d's permitting hypothesis testing in terms of phenomena (e.g. density dependence) that influence both the mean and the standard deviation of production.

Estimation of the Just–Pope Equation

Just and Pope (1978, 1979) present details on the estimation of the above equation. Briefly the function $Y = f(X) + h^{\frac{1}{2}}(X) \exp(V)$ can be estimated using a three stage process.

Stage 1: Estimate the parameters of $f(X)$ — C_4, k_4, d_4 — using the regression

$$Y = f(X) + U^*$$

where U^* is an initial estimate of the error terms equaling $h^{\frac{1}{2}}(X) \exp(V)$.

Stage 2: Estimate the parameters of $h^{\frac{1}{2}}(X)$ — C_5, k_5, d_5 — using the regression

$$|U^*| = h^{\frac{1}{2}}(X) \exp(V).$$

Stage 3: Estimate revised parameters of $f(X)$ given

$$\frac{Y}{\hat{h}^{\frac{1}{2}}(X)} = \frac{f(X)}{\hat{h}^{\frac{1}{2}}(X)} + V.$$

where $\hat{h}^{\frac{1}{2}}(X)$ are the predictions from $h^{\frac{1}{2}}(X)$ estimated at the observed values of X.

Just and Pope (1978, 1979) show that the estimates from the third stage constitute asymptotically efficient estimates of the parameters of $f(X)$ and their standard errors (i.e. the relationship explaining mean yield), and that the estimates from the second stage are consistent estimates of $h^{\frac{1}{2}}(X)$ and their standard errors except for the constant term. The proper constant term is found by multiplying the constant in $h^{-\frac{1}{2}}(X)$ by $e^{-0.6502} = 52.9$ following Just and Pope (1979) and Harvey (1976).

Several comments are in order regarding this procedure. First, it is basically the standard heteroscedasticity correction procedure used for regression models (see Judge et al. (1980, p. 136–142), Kmenta (1971, p. 264–267), and Harvey (1976) for references and discussion). Second, the Just–Pope approach terminates after Stage 3; however, we found it attractive to take the revised estimate of $f(X)$, and then reestimate $h^{\frac{1}{2}}(X)$ until $f(X)$ and $h^{\frac{1}{2}}(X)$ converged. This took one further iteration in the empirical cases below. (Note that the further iterations with this procedure are purely heuristic. The asymptotic large sample properties of the estimates do not change. However, in our smaller samples we did get seemingly better estimates (with decreases in coefficient standard errors).) Third, the above presentation is valid for data that are not expected to be influenced by error components which affect subsamples of the data (i.e. pooled time series and cross sectional data). Just and Pope (1979) present details on estimation in such a case. Fourth, statistical tests may be done at either the second or third stages to determine the importance of factors as they influence standard error and average production.

Data

The following two independent sets of data on production of seaward migrating juvenile salmon and adult returns were used:

Chum salmon — Total Hokkaido Island (Japan) hatchery chum fry releases are used in conjunction with total brood year adult returns (Moberly and Lium 1977). Data are for brood years 1950 through 1969 (sample size 20). This is the same data set used by Peterman (1978, 1981) and is further described in those two papers.

Coho salmon — All data used in this analysis come from the coho salmon plan prepared by the Oregon Department of Fish and Wildlife (1982). Data used are (a) the total number of adults as depicted by the Oregon Production Index (OPI), which is the combined number of adult coho that can be accounted for within the general area south of Ilwaco, Washington for the years 1958 through 1979 (sample size 21); (b) the number of smolt releases is taken from the sum of hatchery releases and an estimate of wild smolt migrants from the Columbia River and the Oregon coast; and (c) a measure of environmental variation is used herein — the Oregon Upwelling Index (OUI). Peterman (1981) used a related data set without upwelling. The inclusion of this factor is motivated by previous work indicating its importance (Gunsolus 1978; Oregon Department of Fish and Wildlife 1982; Clark and McCarl 1983; Walker et al. 1983).

Results

The function used to analyze the relationship between adult production of Hokkaido chum salmon and the mean variability of fry is:

$$A = CS^{k} + dS^{f} \exp(V)$$

The estimation (Table 1) yields the equation:

$$A = 0.0085\, S^{1.09} + (0.3 \times 10^{-6})\, S^{2.54} \exp(V)$$

with standard errors as given in Table 1.

The results from the first stage estimation (identical to Peterman's additive specification) on the average production might have suggested the possibility of density dependence, i.e. that $k_0 = 0.52$ was significantly different from 1.0 (i.e. any acceptance probability greater than 0.09 would lead to rejecting equality). Revised estimates lead both to larger values of k and smaller standard error terms. Consequently the null hypothesis of density independence is accepted (i.e. k_2 is not different from 1 with a probability of 0.04).

The Just–Pope technique provides an estimate of the standard deviation and allows hypothesis testing on the effect of the independent variables on standard deviation. For example, if the effects of smolts on variation was such that we expected an additive error term, then the parameter estimates of the exponents in the multiplicative term involved in $h^{\frac{1}{2}}(X)$ should not be significantly different from zero. However, this is not true for fry in this equation; i.e. the estimate of e_1 is significantly positive (probability greater than 0.995). As the number of chum fry increases by 1%, the standard deviation of adult production increases by 2.5%.

TABLE 1. Estimation results obtained applying Just–Pope procedure to the Hokkaido chum data predicting adult population (A) mean and standard errors (SE) as a function of fry abundance (S).

Comment	Equation estimated	Parameter	Estimate	SE	Parameter	Estimate	SE
Initial mean	$A = C_0 S^{k_0} + U_0^*$	C_0	0.20	0.39	k_0	0.52	0.33
First SE	$\lvert U_0^* \rvert = d_1 S^{e_1} \exp(V_{11})$	$\log d_1$	−8.18	2.55	e_1	1.48	0.45
Revised mean	$A/(d_1 S^{e_1}) = C_1 S^{k_1}/(d_1 S^{e_1}) + V_{21}$	C_1	0.025	0.034	k_1	0.89	0.25
Second & final SE	$\lvert U_1^* \rvert = \lvert A - C_1 S^{k_1} \rvert = d_2 S^{e_2} \exp(V_{12})$	$\log d_2$	−14.37	3.53	e_2	2.54	0.63
Third & final mean	$A/(d_2 S^{e_2}) = C_2 S^{k_2}/(d_2 S^{e_2}) + V_{22}$	C_2	0.0085	0.010	k_2	1.09	0.232

NOTE: The d values are still in logs and have not been adjusted to remove bias.

TABLE 2. Estimation results obtained applying Just–Pope procedure to the Oregon coho data predicting adult population (A) mean and standard error (SE) as a function of smolt abundance (S) and upwelling (Z).

Comment	Equation estimated	Constant			Smolts			Upwelling		
		Parameter	Estimate	SE	Parameter	Estimate	SE	Parameter	Estimate	SE
Initial mean	$A = C_0 S^{k_0} Z^{r_0} + U_0^*$	C_0	0.029	0.045	k_0	0.25	0.31	r_0	0.62	0.21
First SE	$\lvert U_0^* \rvert = \lvert A - C_0 S^{k_0} Z^{r_0} \rvert = d_1 S^{L_1} Z^{M_1} \exp(V_{11})$	$\log d_1$	−9.89	4.28	L_1	1.19	0.89	M_1	0.77	0.77
Revised mean	$A/(d_1 S^{L_1} Z^{M_1}) = C_1 S^{k_1} Z^{r_1}/(d_1 S^{L_1} Z^{M_1}) + V_{21}$	C_1	0.042	0.026	k_1	0.23	0.12	r_1	0.57	0.16
Second & final SE	$\lvert U_1^* \rvert = \lvert A - C_1 S^{k_1} Z^{r_1} \rvert = d_2 S^{L_2} Z^{M_2} \exp(V_{12})$	$\log d_2$	−10	3.89	L_2	2.04	0.8	M_2	0.24	0.71
Third & final mean	$A/(d_2 S^{L_2} Z^{M_2}) = C_2 S^{k_2} Z^{r_2}/(d_2 S^{L_2} Z^{M_2}) + V_{22}$	C_2	0.49	0.027	k_2	0.24	0.12	r_2	0.53	0.16

The Oregon coho estimation was done with a slightly more complex functional form which contains both smolt population and an estimate of upwelling. The equation estimated is: $A = CS^k Z^r + dS^L Z^M \exp(V)$. The results (Table 2) yield the estimated equation:

$$A = 0.049\, S^{0.24} Z^{0.53} + (0.2 \times 10^{-4}) \times S^{2.04} Z^{0.24} \exp(V)$$

with standard errors as given in the table.

The adjustment occurring between the first and third stages in the Oregon coho case does not change the interpretation of potential density dependence (i.e. the practical interpretation of the statistical difference of the k parameter from one). However, it does change the interpretation regarding the contribution of smolt releases to production (i.e. the relationship of the parameter k to zero). Initially k was not statistically different from zero (probability equal to 0.225); however, after application of the Just–Pope procedure the standard error of k declined markedly and k became significantly different from zero (probability of equality is 0.014).

The statistical results suggest that upwelling is not a statistically significant parameter in determining standard error (probability that M_2 equals zero is 0.34). However, the incremental effect on the standard error due to an increase of the number of smolts is significant (probability it equals zero is 0.011): for a 1% increase in smolts released, one obtains a 2.04% increase in the standard error. As was the case for Hokkaido chum, this result causes us to reject the hypothesis of an additive error term in the smolt-to-adult variability relationship.

The Just–Pope procedure has substantially more impact on the Hokkaido chum data estimates than on the Oregon coho estimates. However, this is to be expected. The Just–Pope procedure is essentially a procedure for dealing with heteroscedasticity. Peterman (1981) found heteroscedasticity to be significant in the Hokkaido chum case and insignificant in the Oregon coho case, where the error term is assumed to be additive. Consequently, the estimates of the parameters in succeeding stages showed that there was much improvement to be made by adjusting for heteroscedasticity in the Hokkaido chum case but not nearly as much in the Oregon case.

Since the Hokkaido chum data present an opportunity to improve over a simple additive error term model by following either our approach or changing the model specification as suggested by Peterman, we show both adjustments in Fig. 1. While Peterman's analysis correctly leads him to reject the hypothesis that $k \neq 1$, our estimation gives a corrected estimate of k which actually approaches 1. Further Fig. 1 shows a rather dramatic difference subsequent to the heteroscedasticity correction.

Concluding Comments

Our results support the hypothesis of density-dependent marine survival for Oregon coho salmon. This finding contrasts with analyses by Peterman (1981) and Clark and McCarl (1983) who found no statistical evidence of density dependence in this group of fish. Biologists in the Oregon Department of Fish and Wildlife have attempted several model specifications and manipulations in data sets with

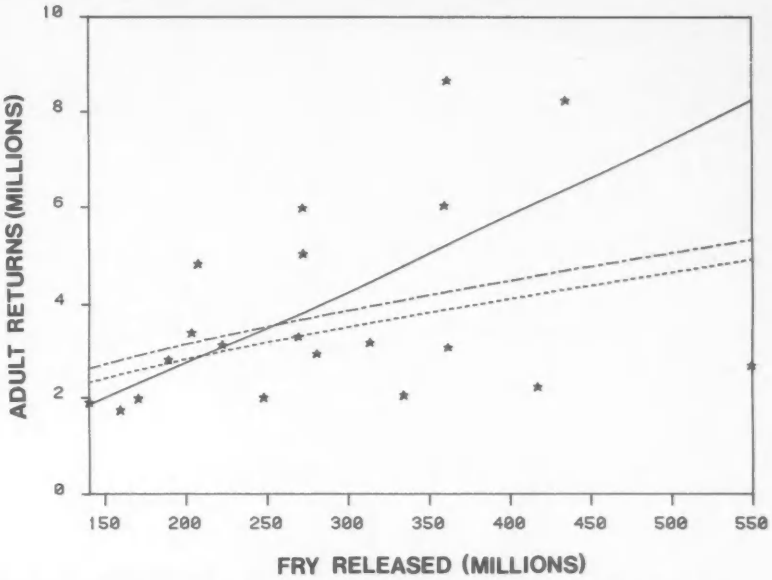

FIG. 1. Relationship between Hokkaido chum fry and adult returns. * gives actual data points; ----- , first-stage (additive error term model) estimate ($y = 0.15x^{0.55}$) Peterman's model 1; ——— , third-stage estimate ($y = 0.0085x^{1.09}$); — · — · , multiplicative error term model estimate ($y = 0.2x^{0.52}$) Peterman's model 2.

widely varying conclusions about density dependence. In fact, at the time this article was written personal communications with several of those biologists suggest that significant differences of opinion remain. Apparently changes in the functional form specification lead to these different conclusions. This places in doubt the value of much of the work on density dependence with small sample sizes. The only way to resolve the density dependence issue appears to be through an expansion of both the quantity and quality of data.

The estimation above, if accepted as valid in the face of the sample sizes, provides interesting information regarding variability. Namely the standard deviation of the total number of adults observed in the fishery increases as a function of the number of smolts. In both data sets the standard deviation increased with the square of the number of releases. Increasing variability implies that the confidence interval on adult production increases as the number of smolts released. This phenomenon would imply that the more fish that are released, the louder would be the fishermen's screams of dissatisfaction about the year-to-year variability of catch. This may indicate that any risk-averse agency may wish to reduce the number of fish released to lessen some of this dissatisfaction. Also it may indicate that participants in the fishery may wish to obtain a more stable total catch by a reduction in the total amount of fish in the fishery. However, these variability reductions would come at a cost in terms of average adult production given the estimates of the data done here.

Finally, if systematic data could be gathered regarding adult production, environmental factors, and many of the parameters which man can influence (such as degree of smoltification), then the use of the variability estimating techniques employed here would provide a basis for fishery agencies to manage variability. The Just–Pope technique allows one to obtain estimates on factors affecting variability and also provides a statistical basis to explore the significance of such factors. Resource managers could follow the suggestions of Walters (1975) who stated that an alternative to sacrificing the high returns is to incorporate the effects of environmental variability and judgmental uncertainty about future production parameters into the design of optimal harvest strategies. Implementation of an attempt to factor in variability could be scientifically supported by estimates of variability such as are developed in this paper.

Acknowledgments

We thank R. Peterman for providing us with data, clarifying his own work, and offering helpful suggestions. Steve Buccola, L. J. Moffitt, and Biing-Hwan Lin provided critical advice on several issues. This work is a result of research sponsored (in part) by the Oregon State University Sea Grant College Program supported by NOAA Office of Sea Grant, U.S. Department of Commerce, under grant number NA 81AA-D-0086.

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Periphyton Biomass and Species Composition in a Coastal Rainforest Stream in British Columbia: Effects of Environmental Changes Caused by Logging

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SHORTREED, K. S., AND J. G. STOCKNER. 1983. Periphyton biomass and species composition in a coastal rainforest stream in British Columbia: effects of environmental changes caused by logging. Can. J. Fish. Aquat. Sci. 40: 1887–1895.

Periphyton biomass, species composition, and accumulation rates on Plexiglas substrates were determined in a 6-yr study from 1974 to 1979 in Carnation Creek, Vancouver Island, B.C. During the first 2 yr of the study, the watershed was unlogged. Clearcut logging during the remainder of the study resulted in increases in light intensity of over 100% at some sites, slight increases in stream temperature (2–3°C in summer) and increases in some dissolved ion concentrations. Phosphorus concentrations were similar throughout the study. Diatoms were the most common class of algae, and *Achnanthes minutissima* and *Synedra rumpens* were the most common diatoms. Filamentous chlorophytes (predominantly *Mougeotia* sp. with some *Draparnaldia* sp., *Spirogyra* sp., and *Zygnema* sp.) occurred sporadically throughout the study but were more common after logging, primarily as a result of increased light intensity. Although highest recorded periphyton biomass and accumulation rates occurred after logging, post-logging values were generally similar to those recorded prior to logging. We attributed this to the lack of increase in phosphorus concentrations after logging.

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Au cours d'une étude de 6 ans, de 1974 à 1979, la biomasse périphytonique, la composition par espèce et les taux d'accumulation sur des substrats de Plexiglas ont été déterminés dans le ruisseau Carnation, dans l'île Vancouver (C.-B.). Pendant les deux premières années de l'étude, il n'y a pas eu d'exploitation forestière dans le bassin de ce cours d'eau. À la suite d'une coupe à blanc pendant la balance de l'étude, l'intensité lumineuse augmenta de plus de 100 % à certains sites, la température du cours d'eau augmenta légèrement (2–3°C en été), de même que les concentrations de certains ions dissous. Les concentrations de phosphore sont demeurées les mêmes pendant toute l'étude. Les diatomées étaient la classe d'algues la plus commune, et parmi celles-ci, *Achnanthes minutissima* et *Synedra rumpens* prédominaient. Les chlorophytes filamenteux (surtout *Mougeotia* sp., avec quelques *Draparnaldia* sp., *Spirogyra* sp. et *Zygnema* sp.) ont été rencontrés de façon sporadique pendant toute l'étude, mais ils ont été plus abondants après la coupe, principalement par suite d'une intensité lumineuse accrue. Bien que les maxima de biomasse périphytonique et de taux d'accumulation enregistrés se fussent produits après la coupe des bois, les valeurs après l'opération ont été généralement identiques à celles d'avant. Nous attribuons ceci à l'absence d'augmentation des concentrations de phosphore à la suite de l'exploitation forestière.

Received April 8, 1983
Accepted July 12, 1983

Reçu le 8 avril 1983
Accepté le 12 juillet 1983

LOGGING of a stream's drainage basin causes major, long-term perturbations in many aspects of the stream environment. Previous studies on the response of periphyton to changes in the stream environment as a result of logging were primarily in western Oregon (Lyford and Gregory 1975; Murphy and Hall 1981). These investigators found increased periphyton biomass after logging, and attributed it primarily to increased light intensity. Hansmann (1969) reported a post-logging reduction in periphyton biomass as a result of reduced substrate availability and altered temperatures. Since edaphic, climatic and attendant physical and chemical factors differ widely between Oregon and the west coast of Vancouver Island (where this study took place), it was thought that different factors could be controlling periphyton biomass, and that the response to logging effects could be different from those observed in Oregon. The objectives of this study were to compare periphyton biomass and species composition on artificial substrates before and after logging of the stream drainage basin. We examined the importance of changes in nutrient supply, flow, light and temperature in controlling biomass accumulation and species composition, and compared these to results from similar studies in the Pacific Northwest.

Certain factors (runoff patterns, annual rainfall, and forest

Printed in Canada (J7321)
Imprimé au Canada (J7321)

FIG. 1. Sampling locations in Carnation Creek and areas of major logging activities.

associations) in Carnation Creek are representative of streams on much of the British Columbia coast (Narver 1974), and it is hoped that results from Carnation Creek may be cautiously extrapolated to many B.C. coastal drainage basins. Findings from this 6-yr study (sample collection 1974–79) will be integrated with those from all components of the multidisciplinary Carnation Creek project (1970–85) in an effort to improve guidelines for coastal logging practices that will provide maximum benefits with minimum damage to the stream environment and the salmonid resource.

Description of Study Area

Carnation Creek (48°55′N, 123°00′W) flows into Barkley Sound on the west coast of Vancouver Island (Fig. 1). Much of the 10 km^2 drainage basin, which contains no lakes, consists of steep slopes rising to a maximum of 700 m in elevation. In winter, snow occasionally accumulates in the higher areas of the watershed, but the duration of snowpack is usually brief. Annual rainfall ranged from 2.6 to 3.6 m and stream flow is highly variable, ranging from <0.03 $m^3 \cdot s^{-1}$ in late summer to >30 $m^3 \cdot s^{-1}$ in some winter freshets. Prior to logging the drainage basin was heavily forested with western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*), and western red cedar (*Thuja plicata*). Logging in selected portions of the drainage basin commenced in the winter of 1975/76 and continued until 1980, although most logging activity took place in the winters of 1976/77 and 1978/79 (Fig. 1). By 1980 approximately 34% of the basin was logged (Anon. 1979).

Methods

Periphyton samplers were placed in a variety of sites within predefined study areas in the creek. Most samplers were located in the lower 2.4 km of the creek, where it passes through a flood plain with an average slope of <2% (Fig. 1). The samplers consisted of rectangular Plexiglas plates (28 × 20 cm) with a 20 × 20 cm sampling area roughened by fine sandpaper. The plates were bolted to concrete blocks approximately 50 kg in weight which were partially buried in the stream bottom. All samplers were oriented with their long axis perpendicular to current direction, and sampling areas were the upper side of the horizontally placed plates. At approximately 1-mo intervals periphyton attached to the sampling area of the plate were removed and placed in a glass jar; periphyton present on other areas of the plate were removed and discarded.

Within 2 h of sample collection, the contents of each jar were split into three portions using a plankton splitter. One portion was filtered onto a Whatman glass fibre filter (GF/C), a few drops of saturated $MgCO_3$ solution were added, and the filter frozen. Filters were later macerated in 90% acetone, and the extracted chlorophyll was measured using a Cary (Model 15) recording spectrophotometer, except for the last 2 yr of the study when a Turner (Model 111) fluorometer was used. Strickland and Parsons' (1972) equation was used to calculate chlorophyll concentrations. Another portion of sample was filtered onto a Whatman GF/C filter which had been ashed and weighed. This filter was frozen and later dried at 100°C to constant weight, weighed, ashed at 460°C for 4 h, and weighed again. Results are expressed as ash-free dry weight (AFDW). The third portion was placed in a glass jar and preserved with Lugol's acetate solution. A portion of this sample was enumerated using a Wild M40 inverted microscope, and algae other than diatoms were identified to the genus level. Cell dimensions and volumes were also calculated and recorded. Permanent quantitative slides of diatoms were made using methods described by Stockner and Armstrong (1971) and diatoms were counted, identified and measured and volumes and relative abundance was calculated. On several occasions during each year of the study qualitative samples of periphyton were collected from natural substrate (rocks) near each stream sampler. Algal species composition was determined from these samples and compared to samples from the nearest stream sampler. More detailed accounts of the biological methods used in this study may be found in Stockner and Shortreed (1976).

Much of the physical and chemical stream data used in this report was collected by other investigators; see Scrivener (1975, 1983) for details. From these data, mean daily stream flow ($m^3 \cdot s^{-1}$) was calculated for the time interval between sampling. However, in a given sampling interval, the occurrence of a freshet just before the sampling date had a considerably greater effect on algal accumulation rates and biomass than a freshet near the beginning of a sampling interval. Since mean daily stream flow gave equal weight to a freshet regardless of when it occurred, it did not adequately describe the

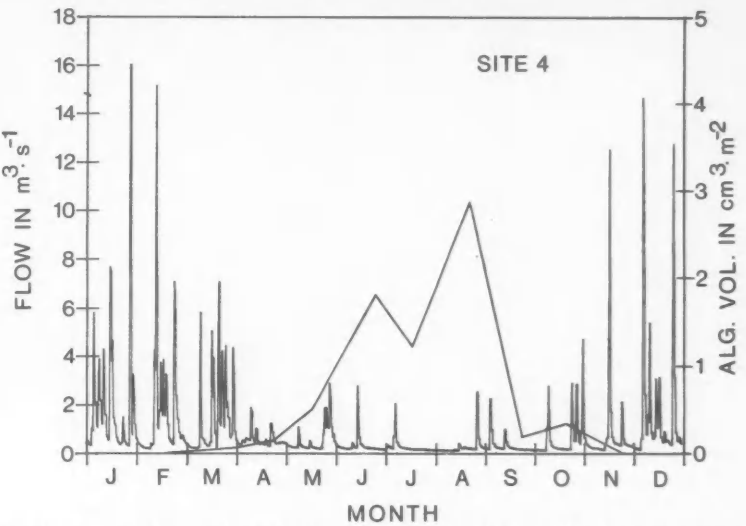

FIG. 2. Annual hydrograph for 1976 and seasonal variation in periphyton cell volume at site 4 for that year.

influence of higher streamflow on algal biomass. Therefore, a flow index (FI) was calculated which gave greater weight to streamflows near to a sampling date. The index was obtained using the formula $FI = \sum_{i=1}^{d} \frac{F_i}{i}$, where d = number of days in a sampling interval, and F_i = maximum daily flow i days prior to a sampling date.

Total incident radiation measurements were taken continuously during the study using a Belfort recording pyrheliometer that was placed on a clear-cut logged hill adjacent to the estuary of Carnation Creek. For each year during the growing season another calibrated pyrheliometer was placed beside each periphyton sampler for a 2-wk period. Percentage of total available light reaching the samplers was calculated from these data.

Results

Stream flow was highly variable in Carnation Creek, both before and after logging, and ranged from <0.03 $m^3 \cdot s^{-1}$ during some summer periods to >30 $m^3 \cdot s^{-1}$ in some winter freshets. On occasion, flow varied by as much as two orders of magnitude in a single 24-h period (Fig. 2). During most years flows were low and stable for approximately a 5-mo period between May–June and September–October, and in this period the greatest periphyton accumulations occurred. Highest mean daily water temperatures in summer were 11–12°C prior to logging and 14–15°C after. Before removal of the forest canopy by logging, light reaching the six sampling sites ranged from 24 to 47% of the total available (Table 1). After logging the percentage of available light reaching the samplers ranged from 46 to 97%. Site 2 was least affected by canopy removal because of its location in a narrow, steep-sided area of the valley bottom. At site 5, effects of logging on light intensity were greatest. The percentage of available light reaching this site increased from 40 to 97%.

Dissolved nutrient concentrations (nitrogen and phosphorus) were variable throughout the study, and changes as a result of logging did not take place until October, 1977. In September, 1977, a 61-ha area which had been logged the previous winter was burned to remove the slash, and after this date nutrient concentrations during freshets tended to be higher than before logging (Scrivener 1983). However, during most low flow periods dissolved phosphorus concentrations were similar to those prior to logging and burning. Nitrate concentrations downstream of the burned areas remained higher than before logging, even during the low flow periods. Nitrate ranged from 2 to 140 $\mu g\ N \cdot L^{-1}$ prior to the fall of 1977 and from 16 to 230 after. Dissolved phosphorus concentrations were more variable after logging (ranging from <1 to 28 $\mu g\ P \cdot L^{-1}$) than they were before, when they ranged from <1 to 9 $\mu g\ P \cdot L^{-1}$. However, average phosphorus concentrations were similar throughout the study.

Periphyton biomass was lowest during times of high and variable flow, as frequent scouring of the streambed occurred at these times. Periods of low, stable flow were required before periphyton could accumulate (Fig. 2). These periods of low flow with stable substrate and limiting scouring coincided with times of high light intensities and maximum temperatures. The seasonal pattern of lowest biomass levels in winter and highest in summer or early fall occurred at all sampling stations throughout the 6-yr study period. Biomass (as chlorophyll) ranged from 0 during high flow periods in winter to >5 $mg \cdot m^{-2}$ during some low flow periods in summer or early fall. Only on one occasion was a concentration of >10 $mg \cdot m^{-2}$ observed. Average growing season chlorophyll values are listed in Table 1.

TABLE 1. Variation in average chlorophyll ($mg \cdot m^{-2}$), in average accumulation rates ($mg\ AFDW \cdot m^{-2} \cdot d^{-1}$), and in the percentage of total available light reaching each sampling site. A = percent light, B = chlorophyll, and C = accumulation rate.

	Site																	
	1			2			3			4			5			6		
Year	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
1974	—	—	—	47	2.26	74	40	1.60	55	39	2.51	77	40	1.77	20	32	3.66	48
1975	—	—	—	—	1.72	26	37	0.70	36	35	1.64	80	44	0.78	13	36	0.72	34
1976	—	2.82	93	—	2.51	51	—	1.54	29	32	2.97	40	41	1.48	22	—	3.54	69
1977	31	6.70	79	24	1.40	31	36	0.80	—	77	0.45	25	95	1.06	19	41	1.32	67
1978	44	2.25	54	24	1.87	25	53	2.78	36	—	4.44	118	97	1.95	55	32	2.86	51
1979	85	4.98	96	46	0.92	38	48	1.65	45	92	—	81	97	0.70	74	71	—	38

Algal accumulation rates (AFDW/days between sampling intervals) ranged from 0 during times of high and variable flow to 0.28 $g \cdot m^{-2} \cdot d^{-1}$ during stable low flow periods in summer or fall. Accumulation rates were generally similar during the pre- and post-logging portions of the study, although after logging accumulation rates were more variable (Table 1, Fig. 3). Highest recorded accumulation rates at most sites occurred after logging. The marked increases in accumulation rates at site 5 in 1978 and 1979 are at least partially due to the changes in current velocity at this site which occurred after large freshets in the fall and winter of 1977. At this site current velocity during low flow periods was 50–60 $cm \cdot s^{-1}$ prior to the winter of 1977/78 and 20–30 after, and the reduction in velocity could account for the increase in biomass (Horner and Welch 1981).

The low average accumulation rates recorded at sites 4 and 5 in 1977 were due to the considerable amounts of small and large organic debris present in the stream after logging, which occurred in this area during the previous winter and spring. For much of this year the streambed was covered by this debris, which remained in the stream until freshets occurred in the fall and winter of 1977.

Common algae during the study were the diatoms *Achnanthes minutissima*, *Synedra rumpens*, *Diatoma hiemale*, *Eunotia pectinalis*, *E. tenella*, *Gomphonema parvulum*, and *Synedra ulna*. Other common algae were the coccoid chlorophyte *Chlorococcum* sp. and the filamentous chlorophytes *Draparnaldia* sp., *Mougeotia* sp., *Spirogyra* sp., and *Zygnema* sp. During periods of high and variable flow (late fall, winter, early spring) and frequent scouring of the substrate, dominant algae were small (<5 μm in diameter) coccoid chlorophytes of which *Chlorococcum* sp. was most common. However, during the growing season (spring, summer, fall) diatoms were usually dominant. *Achnanthes minutissima* was the most common diatom at all sites in Carnation Creek on almost all sampling dates, comprising >60% of total diatom numbers in the majority of instances (Fig. 4). *Synedra rumpens* also occurred at all sites on almost all dates, but seldom comprised >10% of total diatom numbers.

During periods of low, stable flow and high light, filamentous chlorophytes (*Draparnaldia* sp., *Mougeotia* sp., *Spirogyra* sp., and *Zygnema* sp.) occasionally became common. After logging, their relative abundance during these periods increased and they at times formed conspicuous algal "mats" which covered portions of the streambed in logged-over sections of the stream.

The sampling technique used in this study (artificial substrates scraped clean at approximately monthly intervals), appeared to underestimate the abundance of filamentous chlorophytes, and consequently the data do not accurately indicate their actual abundance. However, qualitative observations of the easily visible accumulations of filamentous chlorophytes indicated that their occurrence was both patchy and sporadic, and that after logging diatoms remained the dominant algal group in Carnation Creek.

Qualitative comparisons of periphyton species composition on both artificial and natural substrates indicated that the species composition was generally similar. Diatoms were dominant and *A. minutissima* was the dominant diatom on both

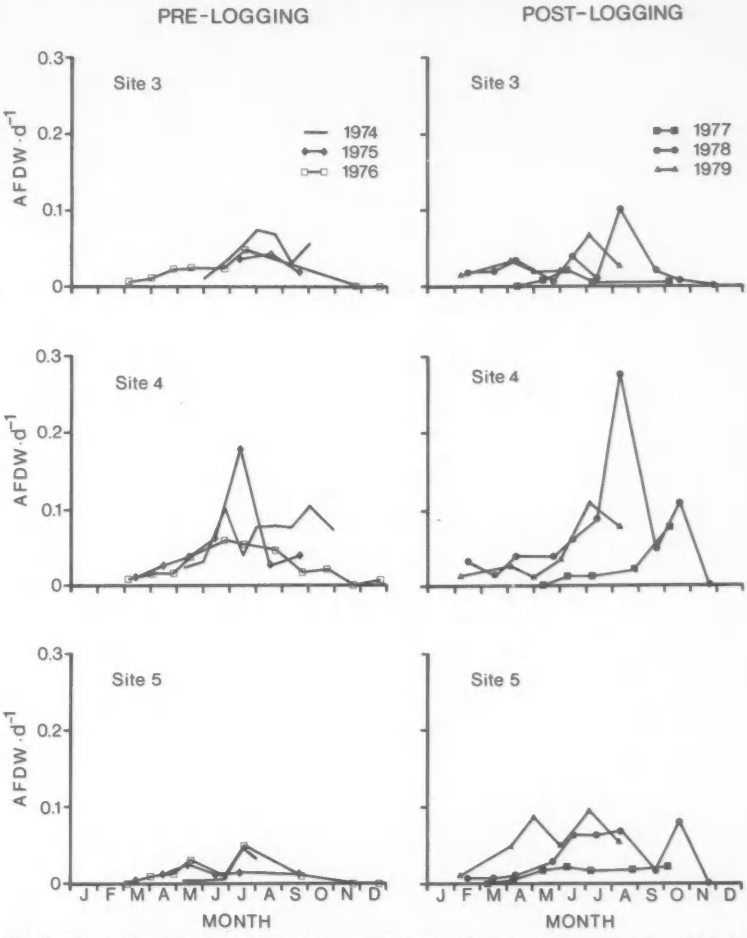

FIG. 3. Seasonal variation of periphyton accumulation rates at three sites during pre-logging (1974–76) and post-logging (1977–79) portions of the study.

substrates (Fig. 5). Other algal species which were common on natural substrate were generally common on artificial substrate. The sole exceptions were the occasions when filamentous chlorophytes became dominant on the natural substrate, and were not as abundant on the artificial substrate.

Discussion

THE HARVEST METHOD

The difficulties associated with obtaining representative, quantitative estimates of periphyton biomass, production, and species composition have been well documented (Weitzel 1979), and the relative merits of artificial and natural substrates have been the subject of considerable debate. It is beyond the scope of this paper to again review the arguments, both pro and con, but we feel it is worthwhile to briefly discuss the utility of data collected by the methods used in this 6-yr study. The "harvest" method, or accumulated growth removed from artificial substrates at regular intervals, has three main disadvantages: (1) periphyton species composition may be qualitatively different than that on natural substrates; (2) accumulated periphyton biomass may be quantitatively different than that on natural substrates; and (3) increased primary production rates could be masked by increased loss rates, and would not be detected by biomass estimates alone. In this study, with the exception of those occasions when filamentous chlorophytes became common, periphyton species composition was generally similar on natural and artificial substrates (Fig. 5). Biomass on natural substrates was

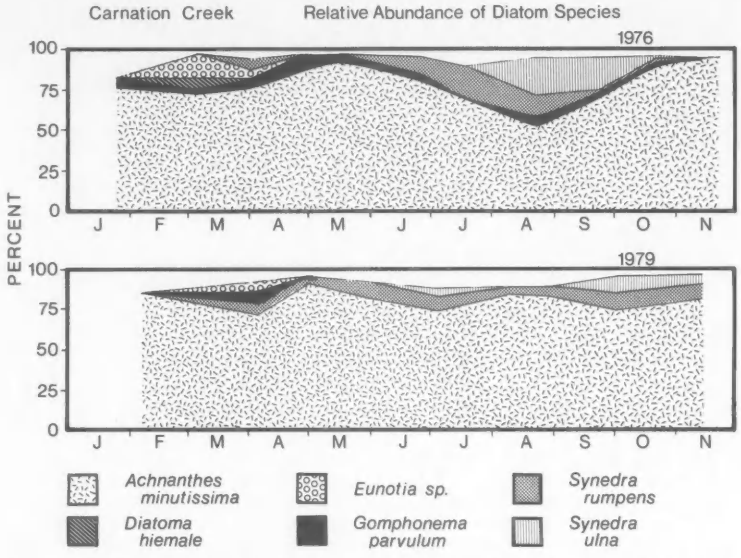

FIG. 4. Seasonal variation of diatom species composition at site 1 during 1976 (pre-logging) and 1979 (post-logging). Data are expressed as percent of total diatom numbers.

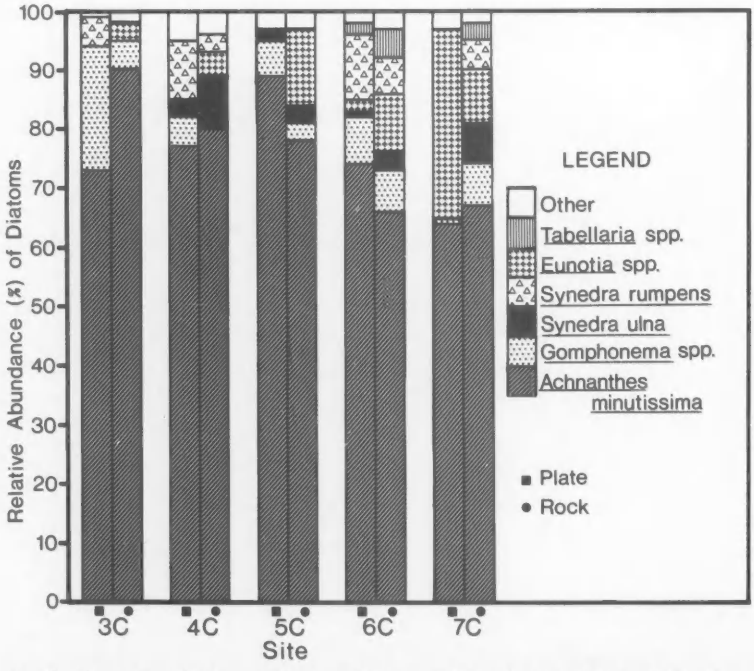

FIG. 5. Comparison of diatom species composition on artificial and natural substrates for five sites on July 17, 1976. Data are expressed as percent of total diatom numbers.

not estimated in this study, so comparisons are not possible, but we do maintain that because of the extreme difficulty in obtaining reliable quantitative samples from natural substrates, artificial substrates are much more suited to obtaining quantitative data which are comparable between years and among sampling sites. Finally, direct estimates of primary production would have been valuable additional information for this investigation; however, the wide variety of techniques used and the lack of standardization among techniques, ensures that comparisons of periphyton primary production rates among investigations would be of little value. Also, there is evidence to suggest that factors such as flow, sediment load, and grazing did not cause increased periphyton loss rates after logging.

Influence of Physical Factors

Of the physical factors known to influence the accumulation rate of periphyton, (light, temperature, flow, substrate quality, and availability) the least important was temperature, as maximum daily summer temperatures increased by only 2−3°C. Phinney and McIntire (1965) found that, given an adequate supply of light and nutrients, periphyton in laboratory streams had a Q_{10} of approximately 2 for the temperature range 6−18°C. An increase of only 2−3°C would not have any detectable effect on periphyton biomass. Streamflow was not affected by logging, as both peak winter flows and low flows during summer were similar before and after logging (Hetherington 1982). However, flow played an important role in limiting periphyton biomass in the stream. While it had little influence on periphyton biomass during the growing season (when flows were low and stable), it did limit the duration of the growing season. The final spring freshet and the first autumn freshet effectively delineated the growing season, although occasional low flow periods of several weeks' duration occurred in winter, and resulted in measurable accumulations of periphyton. When flows were high and variable, losses by scouring were considerable, and periphyton could not colonize the substrate (Fig. 6). When flow index values were >3, accumulation rates were uniformly low. Below a flow index value of 3, other environmental factors were predominant in determining periphyton growth and abundance. The flow index is useful in illustrating the complexity of the relationship between a stream's hydrologic regime and stream periphyton biomass. The occurrence of a freshet on a specific date would have a major influence on algal biomass for several days following the freshet, but the influence would be less marked with each successive day free of freshet. Calculation of the flow index may have value in other stream investigations, particularly in streams subjected to a rapid hydrologic flux. To standardize the flow index among streams, the flow expression could be modified to include drainage basin area (i.e. $L \cdot ha^{-1} \cdot s^{-1}$ instead of $m^3 \cdot s^{-1}$). In Carnation Creek, with a drainage basin area of 10 km^2, the two expressions are equivalent.

Logging activity, particularly the removal of streamside vegetation, contributed to a destabilization of the streambank in Carnation Creek, increased erosion, and a consequent increase in the amount of sediment entering the stream. Scrivener and Brownlee (1980) found an increase in the amount of material <9 mm in diameter in the top layer of

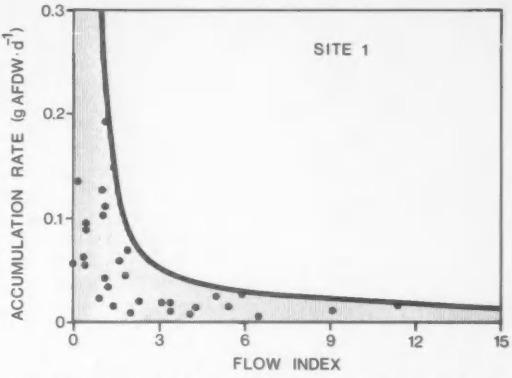

FIG. 6. Variation of algal accumulation rates with the flow index. Data are for all study years from site 1.

gravel in Carnation Creek. This post-logging increase of smaller material has been observed in a number of other systems (Adams and Beschta 1980; Hansmann 1969), and it has generally had a deleterious effect on stream biota. McConnell and Sigler (1959) found it to be a poor substrate for periphyton growth and attachment and Culp (1982) attributed the significant post-logging decreases in macroinvertebrate densities in Carnation Creek to this material. Whereas the samplers used in this study were not affected by substrate size (at least during low flow periods), in some sections of the creek periphyton biomass on natural substrate may have been affected by the reduction in size of natural substrate. Once new vegetation stabilizes the streambanks and reduces input of this fine material, the frequent freshets which occur in the creek should help restore it to the pre-logging condition by removing much of the fine material.

The increased solar radiation which reaches a stream after canopy removal may result in increased periphyton biomass. Gregory (1980), Lyford and Gregory (1975), and Murphy and Hall (1981), found higher biomass in clear-cut logged sections of several Oregon streams than in adjacent, unlogged sections and attributed it to higher average light intensities, since nutrient concentrations were not considered limiting (phosphorus concentrations were 10−200 times higher than those found in this study). However, after logging of the Carnation Creek watershed, chlorophyll concentrations in adjacent shaded and unshaded areas remained similar (Culp 1982). In addition, algal accumulation rates were generally similar before and after logging (Fig. 3). The lack of response to post-logging increases in light intensities suggests that light was not limiting autotrophic production in Carnation Creek.

Influence of Nutrients and Grazing

Increases in dissolved inorganic nitrogen concentrations after logging and slash burning have been detected in a number of studies (Brown et al. 1973; Likens et al. 1970), and were also found in Carnation Creek (Scrivener 1983). The lack of periphyton response to these increases corroborates the conclusions of Stockner and Shortreed (1978), who found in a nutrient enrichment experiment that increased nitrate

concentration had no effect on either periphyton biomass or species composition in wooden troughs carrying Carnation Creek water.

Although post-logging concentrations of dissolved phosphorus in Carnation Creek were more variable than pre-logging values, pre- and post-logging averages were similar, and significant increases did not occur after logging (Scrivener 1983). Throughout the study, any detected increases in dissolved phosphorus concentrations occurred during freshets, when scouring of the streambed (and of the samplers) precluded any periphyton response to increased nutrient concentrations. Stockner and Shortreed (1976) hypothesized that phosphorus was the primary factor limiting periphyton growth rates and biomass in Carnation Creek and later demonstrated (Stockner and Shortreed 1978) that additions of phosphorus (either alone or with nitrogen), increased periphyton biomass while additions of nitrogen only did not. The relatively large changes in some environment factors (light and nitrate) which occurred after logging, and the lack of a periphyton response to these changes, lend support to the earlier hypothesis that during low flow periods, phosphorus is the major factor limiting periphyton production and biomass in Carnation Creek. Because dissolved phosphorus can be taken up very rapidly by algae (Gregory 1978; Lean and Nalewajko 1979; Lehman and Sandgren 1982; McColl 1974), increased phosphorus inputs during low flow periods may not have been detected in the chemical analyses we used. However, the general lack of increase in periphyton biomass during low flow periods supports the conclusion that phosphorus inputs were similar throughout the study.

Although grazing by benthic invertebrates can play a major role in controlling periphyton biomass and production (Cuker 1983; Hunter 1980), it did not appear to be of any significance in Carnation Creek. Qualitative examination of the gut contents of stream benthos (J. C. Scrivener, unpublished data) indicated that while periphyton were utilized, allochthonous detritus was the major food resource. In addition, Culp (1982) found that invertebrate densities were highest in portions of the stream which had the highest standing crops of benthic detritus. Finally, it is unlikely that changes in the invertebrate community after logging would have masked changes in the periphyton community since the density of stream invertebrates was significantly reduced after logging (Culp 1982).

Algal Response

In our study diatoms remained the dominant taxa and the same species were dominant throughout the 6-yr study, although filamentous green algae became more common after logging. In a number of Oregon streams filamentous algae were more common in clear-cut logged sections than in adjacent unlogged sections, although diatoms remained the dominant taxa in all study areas (Lyford and Gregory 1975). In a clear-cut logged stream (Ritherdon Creek) adjacent to Carnation Creek, which had similar nutrient concentrations, filamentous greens were more common than in Carnation Creek prior to logging (Stockner and Shortreed 1976). In addition, although a nutrient enrichment experiment prior to logging in the Carnation Creek drainage basin increased periphyton biomass (Stockner and Shortreed 1978), the relative abundance of filamentous greens did not increase under the experimental conditions (low light, increased nutrients). The similarity of the filamentous green response to logging in Carnation Creek and in Oregon streams, despite widely different water chemistries, is evidence of their greater affinity for high light intensities than many other species of stream periphyton, regardless of ambient nutrient levels.

We conclude that environmental factors that were changed as a result of logging (light intensity, nitrogen concentration, sediment load) had little effect on the periphyton community, because the major limiting factor, phosphorus concentration, was not generally affected. Changes observed in stream benthos and in the stream fish community after logging (Culp 1982; Holtby and Hartman 1982) were clearly a result of changes in the physical environment (increased streambank erosion and temperature), rather than a result of changes in periphyton biomass or species composition. In nutrient-limited, fast-flushing coastal streams such as Carnation Creek, the efficacy of nutrient enrichment in stimulating autotrophic production and providing an increased food resource for stream benthos should be investigated. If such experiments were successful the negative effects of logging on the stream ecosystem could be considerably reduced.

Acknowledgments

Many people gave generously of their time and expertise in various aspects of this study, and although it is not possible to name them all, most prominent are B. Anderson, R. Carr, J. Culp, R. Leahy, and C. Scrivener. We are grateful to E. MacIsaac for assistance in development of the flow index. G. Hartman, E. MacIsaac, H. Mundie, and C. Scrivener critically reviewed this manuscript.

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Hydrologic Control of Lake Susceptibility to Acidification

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Two hundred and seventy-five lakes were sampled in the summer of 1979 to assess the factors controlling susceptibility of northcentral Wisconsin lakes to acidification. In addition to direct evaluation of means and ranges of the physical and chemical characteristics, a cluster analysis was carried out using alkalinity, color, and chlorophyll *a* data. Three well-defined clusters emerged that appeared to be controlled by hydrology: A — dominated by surface runoff; B — dominated by groundwater; C — dominated by precipitation. Relationships between morphometric, hydrologic, and terrigenous factors that can influence lake water quality and susceptibility were further examined by discriminant analysis of 18 watershed properties across the three lake clusters. Hydrologic factors were most important in differentiating the low alkalinity and high alkalinity lakes. The potentially sensitive low alkalinity lakes in northcentral Wisconsin lack surface inlets or outlets and their chemistry is closely associated with precipitation chemistry.

EILERS, J. M., G. E. GLASS, K. E. WEBSTER, AND J. A. ROGALLA. 1983. Hydrologic control of lake susceptibility to acidification. Can. J. Fish. Aquat. Sci. 40: 1896 – 1904.

Un total de 275 lacs ont été échantillonnés durant l'été 1979 dans le but d'évaluer les facteurs réglant la susceptibilité des lacs du centre-nord du Wisconsin à l'acidification. En plus de l'évaluation directe des moyennes et des extrêmes des caractéristiques physiques et chimiques, on a effectué des groupements sur la base de l'alcalinité, de la couleur et de la chlorophylle *a*. Trois groupes bien définis qui semblent contrôlés par les conditions hydrologiques sont apparus : A — un groupe dominé par le ruissellement de surface; B — un autre dominé par l'eau souterraine; C — et un troisième dominé par la précipitation. Une analyse discriminante de 18 propriétés du bassin hydrographique dans les trois groupes de lacs a été utilisée pour étudier de façon plus approfondie les relations entre les facteurs morphométriques, hydrologiques et terrigènes pouvant influer sur la qualité de l'eau des lacs et leur susceptibilité. Les facteurs hydrologiques sont ceux qui permettent le mieux de différencier les lacs de faible et de haute alcalinité. Les premiers, potentiellement susceptibles, dans le centre-nord du Wisconsin sont dépourvus d'arrivées d'eau et d'émissaires de surface, et leurs caractéristiques chimiques sont étroitement associées à celles de la précipitation.

Received November 1, 1982
Accepted July 15, 1983

Reçu le 1 novembre 1982
Accepté le 15 juillet 1983

ACIDIC deposition in North America has been shown to be a relatively widespread phenomenon (Likens and Butler 1981), but documentation of effects on potentially susceptible aquatic resources is limited (Glass et al. 1980). The rate of acidification (i.e. susceptibility) may depend on many factors whose relative importance may vary between regions. Defining susceptible aquatic resources is important not only

Printed in Canada (J7104)
Imprimé au Canada (J7104)

for determining the resources at risk and identifying areas to be monitored, but also for increasing our understanding of factors controlling acidification.

Watershed components, including bedrock geology (Galloway and Cowling 1978; Likens et al. 1979; Hendrey et al. 1980; NADP 1982), surficial geology (Shilts 1981), and soil type (McFee 1980) have been used to predict the extent of susceptible aquatic resources in North America. Each of these approaches provides a useful assessment of regional susceptibility; however, one often observes considerably greater heterogeneity in aquatic susceptibility than predicted from such classifications. One possible explanation for misclassifications is that the classification efforts have been conducted at too coarse a scale, and therefore, the problems can be attributed to map resolution errors. An alternative explanation is that other factors are involved in determining aquatic susceptibility. The objective of our study was to examine the relationships between aquatic susceptibility to acidic precipitation and watershed factors in northern Wisconsin, an area containing lakes displaying a broad range of susceptibility.

Study Area

Northern Wisconsin is a region in which a stagnating glacial mass deposited deep outwash sands and coarse tills interspersed with ice-blocks, which left a landscape dotted with several thousand lakes (Martin 1965). The study lakes are included within the Upper Wisconsin River Basin, bounded by the coordinates 46°07′N, 89°09′W to the north and 45°11′N, 89°41′W to the south. Population density is relatively low (9.3 persons/km^2) (Wisconsin Legislative Reference Bureau 1981), despite a 30% increase during the past decade. Although only 3% of the total land area is developed, approximately 40% of the lake shoreline is used as residential land (Wisconsin Department of Natural Resources 1977).

About 90% of the land surface in the region is now forested. A century ago the upland vegetation was dominated by white pine, hemlock, and hardwoods, but most of it was removed during logging and subsequent burning in the late 1800s and early 1900s (Natural Resources Committee of State Agencies 1956). Regrowth of aspen, birch, mixed hardwoods, and a few conifers has taken place, much of it since 1930. Black spruce is common in the wet, peaty areas. The sands and sandy loams in the surface layers have produced mostly acid soils (commonly pH 4−5), with low cation exchange capacities (~10 meq/100 g) (meq = mmol ion/electrical charge) and low base saturation (10−30%). The upland soils are primarily Omega, Vilas, Pence sands, and sandy loams with peatland soils in the depressions (Soil Conservation Service 1979a). Total concentrations of calcium and magnesium in these soils are typically 1−2 meq/100 g (Soil Conservation Service 1979b).

The igneous and metamorphic bedrock underlying these northern Wisconsin counties is part of a southern extension of the Precambrian Canadian Shield. The bedrock is primarily mafic, intermediate, and felsic metavolcanic rocks with lesser amounts of metasedimentary rocks (Mudrey et al. 1982). The bedrock is overlain by the glacial drift, the most recent of which was deposited during the Woodfordian substage of the Wisconsin glaciation. The study area is located almost entirely within the Wisconsin Valley sublobe of the Woodfordian advance. Drift thickness averages 30 m (maximum 70 m) and few bedrock outcroppings are present (Thwaites 1956). The drift is mostly stratified (Thwaites 1929) with sparse calcareous pebbles found in the deeper, older drift (Broughton 1941; Juday and Meloche 1944). Most groundwater discharging into lakes and streams passes through the glacial drift, with little or no contribution from the bedrock (Oakes and Cotter 1975). Because most of the lakes occur in pitted glacial outwash or end moraines, they are generally shallow, averaging about 10 m in maximum depth and rarely exceeding 30 m. Most of the lakes in the region are thus situated in thick glacial till above bedrock.

The annual precipitation and evapo-transportation average about 80 and 50 cm, respectively (Oakes and Cotter 1975). The recent pH of the rainfall has averaged 4.7 annually compared with an estimated 5.6 in the middle 1950s (Glass et al. 1982; Likens and Butler 1981). The climate is cool and wet, with mean July temperatures of 19°C and January temperatures of −11°C (Burley 1964). The lakes commonly are ice-covered from late November to late April.

Methods

We sampled 275 lakes representative of the aquatic (recreational) resources in the region during summer 1979. Lake selection was intentionally biased to include most lakes in the study area with surface area greater than 100 ha (ranging to as small as 3.9 ha) for which no recent water quality data were available. Shoreline access was required in selection of lakes too small to accommodate a float plane. The study lakes include 45% of the lakes with a surface area greater than 7 ha.

To answer questions about lake/watershed relationships, both in-lake and watershed measures were obtained. Within the lake, conductance and temperature profiles were taken at the deepest point to define thermo- and chemo-clines, using a Yellow Springs Instrument model 33-SCT meter. Integrated water samples were collected from the upper 2 m using a 2.5 cm diameter Tygon tube and were kept on ice and in the dark until analyzed for other chemical properties. Field pH measurements were made with an Analytical Measurement Meter model 707-B, calibrated using pH 4.00 and 7.00 buffers three times per day or every third lake, whichever was less. Split samples were delivered to a private laboratory (Northern Lake Services, Inc., Crandon, WI) within 8 h and to the U.S. Environmental Protection Agency (EPA), Environmental Research Laboratory in Duluth, Minnesota, within 24 h. The laboratory analyses, or appropriate sample preservation, began immediately upon receipt of the sample. Standard methods (American Public Health Association 1975; U.S. Environmental Protection Agency 1979) were used, except where noted otherwise.

In the laboratory, alkalinity was determined by potentiometric titration using Gran plot endpoint methodology. Chlorophyll *a* was determined both monochromatically (corrected for pheophytin) and trichromatically (not corrected for pheophytin), using a Bausch and Lomb model 88

spectrophotometer. The spectral band-width of this instrument is approximately 8 nm; consequently, recovery of chlorophyll *a* was about 88% (R. Martin, Wisconsin Department of Natural Resources, Madison, Wisconsin, personal communication). Turbidity (Hach turbidimeter 1860) and apparent color (Hach DK-2 spectrophotometer model 2582-00 and Hellige Aqua Tester model 611-A with low and high range color wheels) were measured by Wisconsin Department of Natural Resources (WDNR) staff in Rhinelander, Wisconsin. Apparent color (unfiltered) rather than true color (filtered or centrifuged) was measured using platinum color units (pcu). Apparent color averaged ~2 pcu higher than true color based on 944 samples from 60 northern Wisconsin lakes sampled in 1980 (J. M. Eilers and G. E. Glass unpublished data). Replicates were collected randomly for quality assurance for 15% of the samples analyzed by U.S. EPA and 8% of the samples analyzed by Northern Lake Services, Inc.

Over an extended period following the field water sampling, complete physical information for each of the 275 lakes and watersheds was determined using a variety of procedures. Total watershed and lake area were delineated on USGS topographic maps (scale 1:24 000) using an electronic planimeter. Mean lake depth was derived from these area measurements and lake volume data on published WDNR lake bathymetric maps. Where no bathymetric maps were available, mean depth ($\bar{z}$) was estimated using the following regression equations derived from data on maximum depth (z_{max}) for 191 lakes within the study area.

For type I lakes: $\bar{z} = 1.30 + 0.33\ (z_{max})$
$r^2 = 0.78,\ n = 76$

For other lakes: $\bar{z} = 0.71 + 0.35\ (z_{max})$
$r^2 = 0.87,\ n = 115$

Other terrigenous variables were derived from the following sources: surficial geology type (morainal till or outwash) from Hadley and Pelham (1976); depth to bedrock from Oakes and Cotter (1975); soil type, Hole et al. (1968). Broad classes of the dominant vegetation within each watershed were mapped from low altitude aerial photographs taken in 1977 by the Soil Conservation Service (SCS); the data were recorded as percent of the watershed in (i) deciduous cover, (ii) mixed coniferous and deciduous, (iii) bog and associated forest, and (iv) agricultural, urban and other.

Five hydrologic types of lakes were defined based on the relative magnitude of surface water exchange through inlets and outlets:

Type I = no permanent inlets or outlets (groundwater inflow may be very small or moderate);
Type II = intermittent outlet only (groundwater inflow may be moderately strong);
Type III = permanent inlet and outlet (reflecting relatively strong surface water through-flow);
Type IV = permanent outlet and no inlet (reflecting strong spring or groundwater flow); and
Type V = impoundments.

Lake hydrological type was taken from surface water resource publications for Wisconsin counties (Black et al. 1963; Andrews and Threinen 1966; Steuck et al. 1977; Carlson and Andrews 1982) and checked against USGS topographic maps (1:24 000 and 1:62 500) and 1977 SCS low altitude stereo photographs. Field checks of 20% of the lakes confirmed the accuracy of permanent stream identification; however, two lakes which were incorrectly classified as type I contained intermittent outlets and were reclassified as type II lakes. Although impoundments were not distinguished from type III lakes in the original data source, we felt this distinction was important.

The methods used to evaluate relationships between lake susceptibility measures and watershed factors likely to influence water chemistry followed those described by Green (1977). A cluster analysis using alkalinity, color, and chlorophyll *a* as clustering variables reduced the original lake population into a small number of homogeneous groups. As indicated previously, alkalinity is associated directly with lake susceptibility, while the other two are known to be inversely related. The relationships between these lake clusters and environmental factors were explored through discriminant analysis, which, through a simultaneous linear analysis of all the contributing variables, provided identification of factors controlling the separation of lakes in the cluster analysis. Although the three chemical variables used to separate the lakes into clusters and the 18 terrigenous factors used to examine functional control of these groups are not completely independent of one another (correlation coefficients (r) between pairs of water quality measures are alk:color, 0.088; alk:chlor, 0.242; and color:chlor, 0.506), the elements of direct commonality are minimal. Complete absence of linkage is unlikely in a spatial field study of lake chemistry, and this lack of independence is not considered a serious problem for cluster or discriminant analysis (Green 1979).

The statistical analyses of the data were performed using MINITAB (Ryan et al. 1981). Cluster analysis was carried out using CLUSTAN (Wishart 1978), with Ward's (1963) centroid method. Discriminant analysis of the lake groups formed by cluster analysis was done by a single-step procedure (BMDP 1981).

Results

Water Quality Characteristics of the Lakes

An overview of the data for both watershed and water quality characteristics, together with estimates of precision for certain measures, is given in Table 1.[1] The lower limits of alkalinity, laboratory pH, and conductance are −25 μmol/L (negative alkalinity values are equivalent to μmol[H^+]/L), 4.6 and 10 μS/cm, respectively. The low turbidity reflects the surrounding sandy, permeable soils which are not subject to significant erosion. Many lakes have moderately high color values ($\bar{x}$ = 50 pcu) caused by organic acids derived from the incomplete decomposition of plant materials. Juday and Birge (1933) noted that reduced transparency in northern Wisconsin lakes is attributable mainly to the high color values rather than to phytoplankton or inorganic turbidity, a finding corroborated here.

[1]Complete set of tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

TABLE 1. Summary statistics for physical characteristics and the water quality of 275 northern Wisconsin lakes.

Parameter	Median	Mean	Range	Precision[a]
Total watershed area (ha)	274	16899	24–714850	1.6[b]
Lake area (ha)	49	99	3.9–1440	5.2[b]
Shoreline development factor[c]	1.5	1.8	1.0–7.5	—
Maximum depth (m)	6.7	7.8	0.3–29.0	—
Mean depth (m)	3.2	3.7	0.2–10.8	0.5
Lake volume ($\times 10^6 m^3$)	1.6	4.1	0.04–70.0	0.3
Watershed cation exchange capacity (CEC) — average, meq/100 g	20	30	5–180	11
pH (lab)	7.2	—	4.6–9.2	0.05
(field)	6.9	—	4.1–8.9	—
Alkalinity (μmol/L)	287	323	−25–1111	8
Conductance (μS/cm @ 25°C)	48	49	10–128	1
Apparent color (pcu)	22	50	0–400	4
Turbidity (NTU)	1.0	2.4	0–19.0	0.2
Total nitrogen (μg/L)	620	710	10–3100	170
Total phosphorus (μg/L)	19	22	3–77	5
Chlorophyll *a* (trichromatic μg/L)	7.1	9.7	0.9–63.2	1.0
Chlorophyll *a* (monochromatic μg/L)	5.6	7.9	0.2–56.5	2.5
Secchi disc (m)	2.3	2.9	0.2–9.4	0.2

[a]Precision calculated as: $\sqrt{1/2n \Sigma di^2}$; where n = number of pairs and d = difference between pairs, i = number of pairs.

[b]Delineation only.

[c]Index of regularity of shoreline where a circle will have a SLD = 1.0.

$$SLD = \frac{S}{2\sqrt{a\pi}}$$ where S = length of shoreline, a = area of lake.

Most current literature has defined chemical susceptibility of lakes to acidification using alkalinity alone (Wright and Henriksen 1978; Hendrey et al. 1980) or as an input variable for the calcite saturation index (CSI) (Kramer 1976). The distribution of laboratory pH and alkalinity values for the study lakes (Fig. 1) shows a sharp discontinuity near pH 7.0, somewhat higher than that observed by Pfeiffer and Festa (1980) for 100 Adirondack lakes. The histogram of the distributions clearly illustrates that a high percentage of the lakes have extremely low alkalinity, yet have pH values that are generally quite high. The non-normal distributions, particularly that of alkalinity, suggest that a distinct subset of lakes occurs within the study area and presumably this subset can be explained by certain physical factors.

Quantitative Development of Lake Clusters

In a previous study, lakes considered most susceptible to acidification had been characterized as having low alkalinity, being unproductive, and low in color (Wright and Henriksen 1978). A disadvantage in using alkalinity or CSI to define susceptible lakes is that they do not account for lake productivity or degree of bog influence. Consequently, we selected an alternative approach to define a subset of the 275 lakes that would have these characteristics by performing a cluster analysis using the three measures, alkalinity (Gran method), chlorophyll *a* (trichromatic method), and apparent color as input variables. The results (Fig. 2) show a potential separation into six clusters, but when the four smaller sets having a dissimilarity coefficient <60 are combined into one, three primary clusters are obtained. Lake groups which fuse at a low dissimilarity coefficient are alike; those joining at a high value have little in common.

Cluster A, the most heterogeneous of the three, includes 97 lakes with moderately hard water, high chlorophyll, and high color (Table 2). The high color and the high watershed-to-lake surface area ratio suggest a dominant influence from surface water inflow and outflow. We will refer to this group as "surface-water dominated." The four subgroups of lakes in cluster A are significantly different from one another ($P < 0.05$) with respect to several physical and chemical parameters, but because the focus of this research is on susceptible lakes, further analysis of these subgroups is not pursued in this study.

The results in Table 2 show that clusters B and C are clear lakes of low productivity (low chlorophyll), distinguished from each other by volume, pH, and alkalinity. Cluster B (76 lakes), with high alkalinity, high conductance and relatively large lake and drainage area, appears to be strongly influenced by waters of groundwater origin ("groundwater dominated"). Cluster C, in contrast, is comprised of lakes with low alkalinity, low dissolved material (i.e. low conductance), small lake area, and a low watershed-to-lake area ratio, suggesting a minimal groundwater influence. The

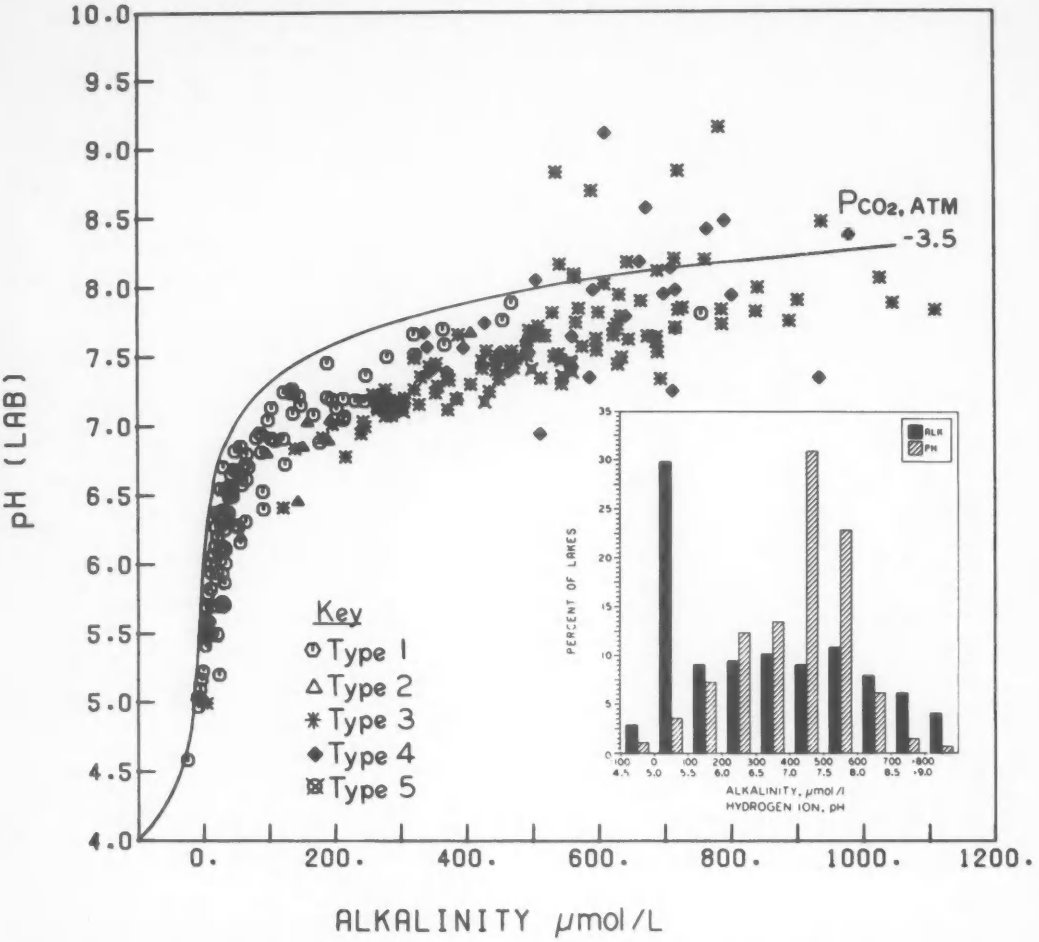

FIG. 1. Distribution of laboratory pH and alkalinity for 275 northcentral Wisconsin lakes. See text for description of lake types listed in the key. The solid line indicates the calculated hydrogen ion–bicarbonate–carbonate relationship for water in equilibrium with atmospheric carbon dioxide (Stumm and Morgan 1981).

median alkalinity is 39 μmol/L, indicating that, as a group, cluster C lakes are highly susceptible to acidic inputs. Although a considerable spectrum of groundwater relationships undoubtedly exists within this group, we have named it "precipitation dominated" in comparison to the other groups. The extremely low concentrations of dissolved materials in cluster C lakes compare closely with that of the precipitation quality as measured by the conductance values (Table 2) 20 and 16 μS/cm at 25°C, respectively. Cluster C, which has all of the characteristics of susceptible lakes, comprises over one-third (102) of the study lakes.

Obviously, slightly different dendograms could have been generated, depending on the clustering algorithm and measure of similarity used. The stability of the clusters was evaluated using several different clustering criteria and also by using pH, alkalinity, and conductance as input variables. In most cases, there was little change in either the number or the composition of the clusters. Statistical tests on the median values for each group indicate that in most cases the medians are significantly different ($P < 0.05$) for all three groups. These tests support the hypothesis that the groups formed by cluster analysis in this study represent significantly different subpopulations of the entire set of lakes. Table 3 summarizes the physical and chemical characteristics of the lakes grouped by hydrologic type alone and indicates the statistical significance for these measures.

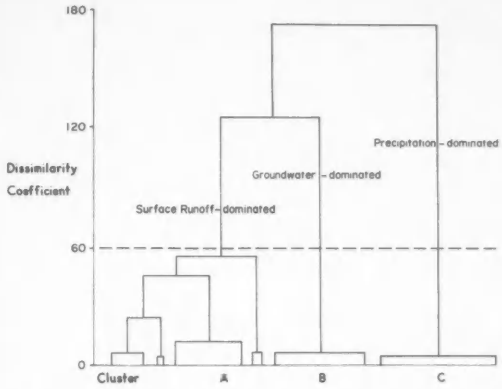

FIG. 2. Dendrogram for 275 lakes based on alkalinity, color, and chlorophyll.

DISCRIMINANT ANALYSIS OF WATERSHED FACTOR EFFECTS

The relationships between 18 watershed properties and the three water-quality-defined clusters, including the acid susceptible group, were evaluated by discriminant analysis. The functions resulting from the latter incorporate contributions from each variable included in the analysis, such that the maximum separation between designated groups is achieved. The discriminant analysis produced two orthogonal discriminant functions, I and II. Cluster C remained strongly differentiated from clusters A and B (Fig. 3). Watershed variables with correlation coefficients (Table 4) showing large absolute values play important roles in distinguishing between the different levels of lake susceptibility represented by these clusters.

As indicated by the separation of cluster C from clusters A and B in Fig. 3, the discriminant function I accounted for 89% of the total dispersion among the clusters. This function correctly classified 98% of the lakes within cluster C. Hydrologic variables for lake types I ("precipitation dominated") and III ("surface water/groundwater dominated"), showed the highest negative and positive correlations, respectively, with discriminant function I. Lake surface area also showed moderately strong positive correlation with discriminant function I.

Discriminant function II accounted for only 11% of the total dispersion, largely between clusters A and B (Fig. 3, y-axis). The most important variables operating along this axis were watershed area (a variable related to the extent of surface water flow-through), percent bog in the watershed (a variable related to color), and classification in hydrologic

TABLE 2. Physical and chemical characteristics of lake clusters (median).

	Cluster A	Cluster B	Cluster C	Precipitation[a] (Trout Lake)
Number of lakes	97	76	102	
Physical characteristics				
Total watershed area (ha)	1279[b]	400[b]	99[b]	
Lake area (ha)	72	82	24[b]	
Total drainage area/lake area	20.9[b]	5.0[b]	3.4[b]	
Shoreline development factor (SLD)[c]	1.5	1.6	1.5	
Maximum depth (m)	6.1[b]	7.0	6.9	
Mean depth (m)	2.8[b]	3.3	3.5	
Lake volume ($\times 10^6 m^3$)	2.0	3.2	0.9[b]	
CEC, watershed average, meq/100 g	30	20	20	
Chemical characteristics				
pH (laboratory)	7.3[b]	7.8[b]	6.4[b]	4.7
Alkalinity (μmol/L)	345[b]	618[b]	34[b]	−20
Conductance (μS/cm @ 25°C)	54[b]	75[b]	20[b]	16
Apparent color (pcu)	95[b]	19[b]	8[b]	
Total nitrogen (μg/L)	880[b]	570	520	
Total phosphorus (μg/L)	28[b]	20[b]	15[b]	
Chlorophyll a (μg/L)	15[b]	5[b]	4[b]	
Secchi disc (m)	1.2[b]	2.7[b]	3.8[b]	

[a]National Acid Deposition Program monitoring site, volume weighted average values for 1979–82 (Glass et al. 1982).

[b]Significant difference between medians ($P < 0.05$) using a Mann-Whitney U-test with the probability level adjusted for multiple comparisons.

[c]Index of regularity of shoreline where a circle will have a SLD = 1.0.

$$\text{SLD} = \frac{S}{2\sqrt{a\pi}}$$ where S = length of shoreline, a = area of lake.

TABLE 3. Physical and chemical characteristics of lakes by hydrologic type (median).

	Lake type				
	I	II	III	IV	V
Number of lakes	117	9	106	31	12
Physical characteristics					
Total watershed area (ha)	111	250	1904[a]	215	185 446[a]
Lake area (ha)	25	49	84	65	225[a]
Total drainage area/lake area	3.4	5.6	18.1[a]	3.1	552[a]
Shoreline development factor (SLD)[b]	1.5	1.4	1.5	1.4	4.5[a]
Maximum depth (m)	7.0	5.2	6.1	6.7	7.2
Mean depth (m)	3.6	3.0	3.0	2.9	2.8
Lake volume ($\times 10^6 m^3$)	0.9	1.4	2.2	2.0	7.7
CEC, watershed average, meq/100 g	17	40	27	22	8
Chemical characteristics					
pH (laboratory)	6.4	6.9	7.5	7.7	7.4
Alkalinity (μmol/L)	39[a]	160[a]	513	588	496[a]
Conductance (μS/cm @ 25°C)	20[a]	36	64	74	63[a]
Apparent color (pcu)	8[a]	68	64	18	83[a]
Chlorophyll *a* (trichromatic μg/L)	3.9[a]	12.2	10.1	6.2	18.8[a]
Secchi disc (m)	3.7[a]	1.5	1.7	2.3	1.2[a]

[a]Significant difference between all medians ($P < 0.05$) using a Mann–Whitney *U*-test with the probability level adjusted for multiple comparisons.

[b]Index of regularity of shoreline where a circle will have a SLD = 1.0.

$$SLD = \frac{S}{2\sqrt{a\pi}}$$ where S = length of shoreline, a = area of lake.

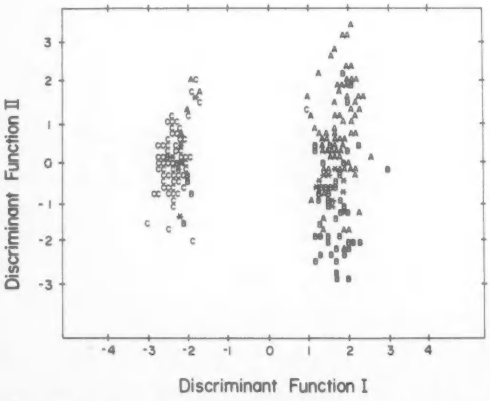

FIG. 3. Results of discriminant analysis for 275 lakes in three clusters. Lake clusters A, B, and C refer to those in Table 2 and Fig. 2.

type IV ("groundwater dominated"). The use of continuous variables rather than categorical data for hydrology, vegetation, soils, and glacial tills might improve the expression of significance of some of these variables, but the differences seem likely to be small.

Surficial geology and soil type, widely used in previous inventories of sensitive areas, were not found to be major factors influencing lake susceptibility in this part of Wisconsin. However, only a modest range of geology and soil types is found here; this inadequately represents the range of conditions used in broad-scale mapping. Indeed, an examination of alkalinity in other northern Wisconsin lakes across glacial lobes shows some influence of glacial origin (Simpkins and Mickelson 1979). Despite the limited range in geologic types, the lake water quality measures show all of the variability found by other studies.

Discussion and Conclusions

These results indicate that because type I lakes are: (i) so different from other lake types, and (ii) nearly as dilute as precipitation, they have little interaction with the watersheds or the groundwater. Thus, maps or inventories of susceptible lakes or regions based on terrigenous factors exclusive of hydrologic processes could be misleading. Second, if the softwater lakes are dominated by precipitation, we conclude that these lakes are more likely to be chemically altered by a change in precipitation chemistry such as a long-term increase in acidic deposition. Third, because the type I lakes have low watershed-to-lake ratios and receive little runoff, they would not be expected to experience short-term pH depressions from episodic events such as spring snowmelt.

An important concern with respect to these study lakes must be to quantify the hydrologic exchanges between the

TABLE 4. Correlation coefficients and percent separation for discriminant functions I and II.[a]

Variables	Discriminant function I	Discriminant function II
Morphometric factor		
Lake area	0.48	0.01
Watershed area	0.34	0.45
Mean depth	−0.24	−0.36
Watershed area/lake area	0.30	0.39
Lake elevation	−0.20	−0.26
Hydrologic type[b]	0.99	0.62
I (no inlet or outlet)	−0.99	0.04
II (intermittent outlet)	0.12	0.24
III (inlet(s) and outlet(s))	0.68	0.04
IV (no inlet, permanent outlet)	0.31	−0.48
V (impoundment)	0.20	0.36
Geology		
Moraine tills (ground and end)	−0.29	−0.20
Outwash plains	0.29	0.20
Depth to bedrock	−0.33	0.49
Vegetation/landuse cover type[b]	0.29	0.53
Agricultural, urban, other	−0.12	−0.14
Bog and forest	0.26	0.49
Deciduous	−0.19	−0.15
Coniferous and deciduous	0.06	−0.25
Soil		
Loam and silt loams	0.01	0.27
Sand	−0.01	−0.27
Percent separation	89	11

[a]Values greater than $|0.13|$ are significant ($P < 0.05$).
[b]Correlation coefficients for group variables represent the best linear combination of the individual variables within the group.

type I lakes and the surrounding more alkaline groundwater. Several investigators have examined the interaction between lakes and groundwater in Wisconsin (Fries 1938; Broughton 1941; Juday and Meloche 1944; Hackbarth 1968; Simpkins et al. 1978) and Minnesota (Hawkinson and Verry 1975; McBride and Pfannkuch 1975; Winter 1978). The early lake/groundwater interpretations, in which lake basins were often classified as "sealed" from the groundwater, have been superseded by more sophisticated concepts of lake/groundwater exchange in which a lake is rarely described as isolated from the groundwater. Furthermore, analysis of lake/groundwater interaction based on a small number of watershed piezometers may not adequately describe a system with large spatial and temporal variability (i.e. having differences in groundwater inflow/outflow across and through the lake bottom, and seasonal and annual fluctuations which may reverse groundwater discharge/recharge relationships). Nevertheless, the water chemistry data and the absence of any strong watershed relationship shown here indicate that many of the type I lakes are influenced only minimally by groundwater.

The type I lakes identified in this study are chemically similar to the group I lakes identified by Gorham et al. (1983) in the north-central United States. However, the results of our study conflict with the conclusions of Gorham et al. (1983) who attributed the differences between the dilute lakes (conductance <29 μS/cm) and the more buffered group II lakes (conductance 29−141 μS/cm) to differences in soil types in the watersheds. No doubt, there are differences in soil types between watersheds for groups I and II; however, when we examined the importance of soil types compared to hydrology within a physiologic unit, the influence of soil was substantially less than that of hydrology.

Although the distinction between susceptible and nonsusceptible lakes in northcentral Wisconsin can be made largely on the basis of surface water inlets and outlets, dividing lakes into seepage and drainage categories will probably not achieve the same results outside this physiographic region. This is evident for the Adirondack region where acidic lakes possess surface inlets and outlets. The results of our analysis indicate that the one important factor susceptible lakes have in common across regions is minimal groundwater input, and not necessarily that they share similar watershed characteristics. Thus, the challenge of accurately assessing lake susceptibility, in part, will be to quantify lake/groundwater interactions.

Acknowledgments

We thank A. Pollack and C. Stidley for assistance in statistical analysis and review. M. Steimle collected most of the samples and laboratory analyses at ERL-D were performed by L. Anderson and C. Sandberg. We thank the following for constructive suggestions on earlier drafts: P. Brezonik, K. Biesinger, T. Winter, G. Niemi, G. Rapp, E. Lange, and O. Loucks. This manuscript was prepared with the assistance of R. Berg, D. Erickson, J. Ilse, F. Simmons, J. Sorensen, S. Tongen, and T. Highland. This work was financially supported by the U.S. Environmental Protection Agency (CR 809484) and the Wisconsin Department of Natural Resources.

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Decline of *Mysis relicta* During the Acidification of Lake 223

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NERO, R. W., AND D. W. SCHINDLER. 1983. Decline of *Mysis relicta* during the acidification of Lake 223. Can. J. Fish. Aquat. Sci. 40: 1905 – 1911.

The population size of *Mysis relicta* in Lake 223 of the Experimental Lakes Area, northwestern Ontario, decreased from 6 700 000 ± 1 330 000 (± 95% confidence limits) during August of 1978, to 270 000 ± 75 000 during August of 1979, a 96% decrease. Because *Mysis*, a cold stenotherm, is restricted to the metalimnion and hypolimnion of lakes during summer, the pH range encountered by the population was 5.51 to 6.32 in 1978 and 5.23 to 6.10 in 1979, even though mean pH values in epilimnion waters for the 2 yr were 5.84 and 5.60. A decrease in pH of its habitat from 6.2 to 5.6 during fall overturn in 1979 caused the elimination of the remaining 4% of the population. Comparisons with four control lakes suggested that the decline and disappearance were not normal occurrences in unstressed lakes. Concentrations of Zn, Al, Mn, Fe, Cd, Cu, Ni, and Hg in Lake 223 water were low, and concentrations in *Mysis* were less than or equal to those in animals from five control lakes, suggesting that the decline in this species was not due to the toxic effects of metals. All size classes were affected, so that direct toxicity of hydrogen ion may be responsible for this abrupt population collapse. These results suggest that *Mysis* may be a useful early indicator of acidification damage to Precambrian Shield lakes.

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L'effectif de la population de *Mysis relicta* dans le lac 223 de la Région des lacs expérimentaux, dans le nord-ouest de l'Ontario, a diminué, passant de 6 700 000 ± 1 330 000 (limites de confiance de ± 95 %) en août 1978 à 270 000 ± 75 000 en août 1979, soit une diminution de 96 %. *Mysis*, un sténotherme froid, est limité au métalimnion et à l'hypolimnion des lacs en été, où le pH rencontré par la population était de 5,51 à 6,33 en 1978 et de 5,23 à 6,10 en 1979, même si les valeurs moyennes du pH des eaux épilimnétiques ces 2 ans-là étaient de 5,84 et 5,60. Par suite d'une diminution du pH de son habitat, qui est passé de 6,2 à 5,6 lors du renouvellement automnal en 1979, les 4 % de la population qui restaient ont été éliminés. Une comparaison avec quatre lacs témoins donne à penser que le déclin et la disparition de cet organisme ne sont pas des phénomènes communs dans des lacs non soumis à des contraintes. Les concentrations de Zn, Al, Mn, Fe, Cd, Cu, Ni et Hg dans l'eau du lac 223 étaient faibles, alors que dans *Mysis*, elles étaient inférieures ou égales à celles observées chez des animaux de cinq lacs témoins, signe que le déclin de l'espèce n'est pas dû aux effets toxiques des métaux. Tous les groupes de taille ont été affectés, ce qui donne à penser que ce brusque affaissement de la population a pu être causé par la toxicité directe de l'ion hydrogène. D'après ces résultats, *Mysis* pourrait être un premier indicateur utile des dommages causés par l'acidification aux lacs du Bouclier précambrien.

Received March 2, 1983
Accepted July 15, 1983

Reçu le 2 mars 1983
Accepté le 15 juillet 1983

MANY Precambrian Shield lakes in southern Canada are believed to be acidified by anthropogenic emissions (Dillon et al. 1978; Dillon et al. 1979; Jeffries et al. 1979; Scheider et al. 1979; Watt et al. 1979; and Harvey 1980). Hendrey et al. (1976) and Okland and Okland (1980) have suggested that the loss of food organisms could stress fish populations well before pH levels became low enough to cause reproductive failure or other direct stresses on the fishes. In deep oligotrophic lakes, *Mysis relicta* is an important food for a number of fish species (Rawson 1961; Dryer et al. 1965; Wells and Beeton 1963; and Bailey 1972). Benthic crustaceans such as *Gammarus lacustris* and *Asellus aquaticus* appeared from the Scandinavian survey work to be very sensitive to acidification (Okland and Okland 1980). *Mysis relicta* was therefore a key organism to study during the experimental acidification of Lake 223 (L223) of the Experimental Lakes Area (ELA), northwestern Ontario (Schindler 1980; and Schindler et al. 1980) in order to determine its sensitivity to acidification.

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Printed in Canada (J7279)
Imprimé au Canada (J7279)

Description of the Study Lakes

Lake 223 is a small oligotrophic lake, 27.3 ha in area with a mean depth of 7.2 m and a maximum depth of 14.4 m. Reference lakes 224, 239, and 305 are slightly larger (25.9, 54.3, and 52.0 ha, respectively) and deeper than 223 (mean depths 11.6, 10.5, and 15.1 m, respectively, and maximum depths of 27.4, 32.0, and 32.7 m, respectively). Lake 228 is a much larger lake of 1677 ha with mean and maximum depths of 55.4 and 167 m, respectively. Additional geographic and morphometric data on the lakes are available in Brunskill and Schindler 1971; Hesslein et al. 1980; and Schindler et al. (1980). Bottom waters in lakes 224, 228, 239, and 305 are oxygen rich during the summer for most years (Schindler 1971; and Schindler et al., unpublished data). Oxygen concentrations in L223 fall below 2 $mg \cdot L^{-1}$ at a depth of 10 m during most summers (Schindler et al. 1980). Lake 223 is also the most productive of the four lakes studied (Fee 1980).

Methods

Population estimates of *Mysis* in L223 were based on quantitative samples collected during August 1978 and August 1979 using nighttime vertical tows of a 1-m^2 net (Nero 1982). The 1978 estimate was based on 82 samples collected along six transects between August 2 and August 27 (Nero and Davies 1982). Similarities in *Mysis* densities among the transects in 1978 (differences not significant, $P = 0.17$, Friedman test, Hollander and Wolfe 1973) led to the use of a single transect in 1979. Forty-five samples were collected, between August 14, and September 9, 1979, from nine permanent stations (at 6.0, 7.0, 8.0, 8.7, 9.8, 10.4, 11.4, and 13.7 m depth) located along a transect running from the north shore of L223 to the center of the lake. Population estimates based on 14 to 23 samples collected along single transects were also made of *Mysis* in lakes 224 (1981), 239 (1979 and 1980), and 305 (1980). Occasional observations made using SCUBA were used to corroborate changes in the *Mysis* population of L223.

Mysids were classed as young-of-the-year or adult based on total animal lengths (≤ 10 and > 10 mm, respectively). Counts were corrected for a measured net collection efficiency of 80%, at a towing speed of 1/3 $m \cdot s^{-1}$. Population sizes were calculated using methods for depth-stratified random sampling (Elliot 1977) with samples collected at the fixed stations treated as random samples from strata defined by depth contours. Population sizes of juveniles and adults were estimated separately and summed to give a total estimate. Because *Mysis*, a cold stenotherm, only occurs in the epilimnion in early spring and late fall, between-lake comparisons were based on the number of *Mysis* per unit surface area below the thermocline during midsummer, to restrict comparisons to the area of the lake available to *Mysis*. The thermocline was regarded as the plane of maximum rate of temperature change per metre of depth (Hutchinson 1957).

The limits of pH encountered by *Mysis* in L223 were determined using a combination of monthly pH, temperature, and oxygen profiles (Schindler et al. 1980, and unpublished data). The portion of the water column and sediment surface normally inhabited by *Mysis*, defined here as the "inhabitable zone," was determined on the basis of the maximum temperature (17.6°C, Nero and Davies 1982) and the minimum of oxygen concentration which the species can tolerate (2 $mg \cdot L^{-1}$, Brownell 1970). Within this inhabitable zone determined from monthly profiles of oxygen and temperature, the highest and lowest pH values were recorded from monthly profiles, and from twice-weekly measurements made in the epilimnion when the inhabitable zone included this stratum. This pH range is normally somewhat higher than that of surface waters due to buffering by microbial processes and sediment–water exchange in the hypolimnion (Schindler et al. 1980; Schindler and Turner 1982; Cook and Schindler 1983).

In L223, samples for life cycle analysis were collected using vertical and horizontal tows of a 1-m^2 net at 1–2-wk intervals from June to September 1978, and during May to September 1979. In the reference lakes 224, 228, 239, and 305, life history samples were collected at 2–4-wk intervals between May 1979 and June 1980. For each animal, the antennal scale length was measured (Grossnickle and Beeton 1979) and the sex and stage of development were recorded. Mean population growth was measured as the mean increase in antennal scale length per month. The mean size at onset of sexual maturity (Wenner et al. 1974) was determined for females aged 1+ yr collected between May 5 and October 1 in 1978, 1979, and 1980.

Metal determinations were carried out on mysids collected from Lakes 223, 224, 228, 239, 305, and 468. All samples were taken in 1979 or 1980 except for the L223 samples, which were taken in summer 1978. No L223 samples from 1979 were analyzed because few *Mysis* were captured. Metals were analyzed by the Analytical Chemistry Unit at the Freshwater Institute, Winnipeg, Manitoba. Aliquots of approximately 0.2 g of dried *Mysis* were digested in teflon beakers by repetitive additions of isothermally distilled concentrated HNO_3, heating beakers gently until only white or pale yellow residue remained. The residue was taken up in a few drops of ultrapure HCl and made up to 25 mL with distilled water. Iron, manganese, copper and zinc were measured by direct aspiration of the aqueous digest into the flame of a Varian AA5 atomic absorption spectrometer. For cadmium and nickel analysis, a portion of the digest was buffered to pH 8.5 with sodium acetate, then extracted into 2 mL of 0.5% diethyl ammonium dithiocarbamate in *n*-butyl acetate. The chelated metal was then analyzed in the above AA spectrometer. Lithium was added to another portion of the digest, after which it was analyzed for aluminium on a Spectrametrics III D.C. argon plasma emission spectrometer.

For mercury, two separate 0.2 g aliquots of *Mysis* were digested in cold nitric:sulfuric permanganate, followed by flameless A.A. (Armstrong and Uthe 1971).

To determine whether storage time affected mean metal concentrations, samples from each lake were ranked according to storage time (scale 1–6). Analysis of variance was used, with metal concentration and storage time rankings as two treatment effects having one observation per cell. Duncan's multiple range test was used to examine differences between the means (Snedecor and Cochran 1967). The storage time of the sample had no significant effect on the mean concentrations of the metals in the *Mysis* ($P = 0.11$ to $P = 0.98$).

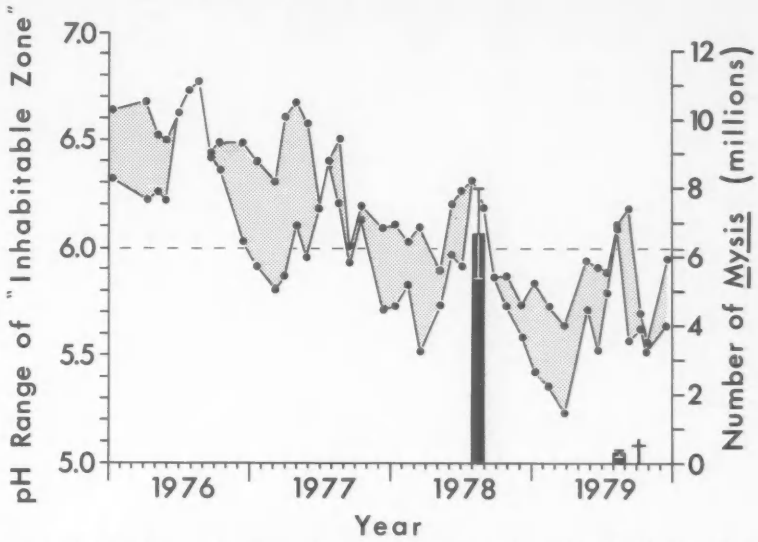

FIG. 1. The maximum and minimum pH found within the water column of L223 inhabited by *Mysis relicta* (represented by shading). Dark vertical bars represent population estimates and their ±95% confidence intervals. The cross indicates date at which *Mysis* were no longer observable in L223.

TABLE 1. Mean densities of *Mysis relicta* as number·m^{-2} of the area below the midsummer thermocline, calculated from whole lake population estimates.

Lake	Date	Number of hauls	Area of thermocline ($\times 10^5$ m^2)	Mean density	±95% conf. limits
223	Aug. 78	82	1.56	42.8	8.52
223	Aug. 79	45	1.48	1.9	0.16
224	July 81	15	1.70	595	40.5
305	July 80	14	3.09	313	74.7
239	July 79	23	4.20	179	13.9
239	Aug. 79	18	4.20	91	20.9
239	July 80	18	4.20	164	73.8
239	Sept. 80	18	4.20	160	96.9

Results

The population of *Mysis* in L223 decreased from 6 700 000 ± 1 330 000 (± 95% confidence limits) in 1978 to 270 000 ± 75 000 in 1979 (Fig. 1). SCUBA observations during the summers of these years corroborated the decrease. During this period, the pH of the water column inhabited by *Mysis* was reduced by artificial acidification from a range of 5.51–6.32 (March and July 1978, respectively) to a range of 5.23–6.10 (March and August 1979, respectively). On October 6, 1979, scuba divers were unable to observe *Mysis* in the lake. The total disappearance coincided with a decrease in the pH from 6.1 to 5.6 in the region inhabited by *Mysis* (Fig. 1, August and September 1979).

The *Mysis* density in L223 in 1978 was below that expected from densities in control Lake 239 for 1979, lakes 239 and 305 for 1980, and L224 for 1981. Mean *Mysis* densities in control lakes ranged from 91·m^{-2} to 595·m^{-2} (Table 1), with an overall mean of 244·m^{-2}. By comparison, the summer, 1978 mean of 42.8 *Mysis*·m^{-2} in L223, suggests that either low oxygen conditions in L223 had always limited population size or that some decline from pre-acidification years to 1978 might have occurred. During the winter of 1977–78 the pH of the water column inhabited by *Mysis* did occasionally drop below pH 6 (Fig. 1).

The adult proportion of the population was also lower in L223 than in reference lakes. Only 7.0 and 12.6% of the *Mysis* in L223 were adults in 1978 and 1979, respectively, compared with 18–54% for populations in Lakes 224 (1981), 239 (1979, 1980), and 305 (1981). *Mysis* in all these lakes have a similar two year life cycle. The life cycle and growth rate of *Mysis* in L223 otherwise appeared normal prior to their

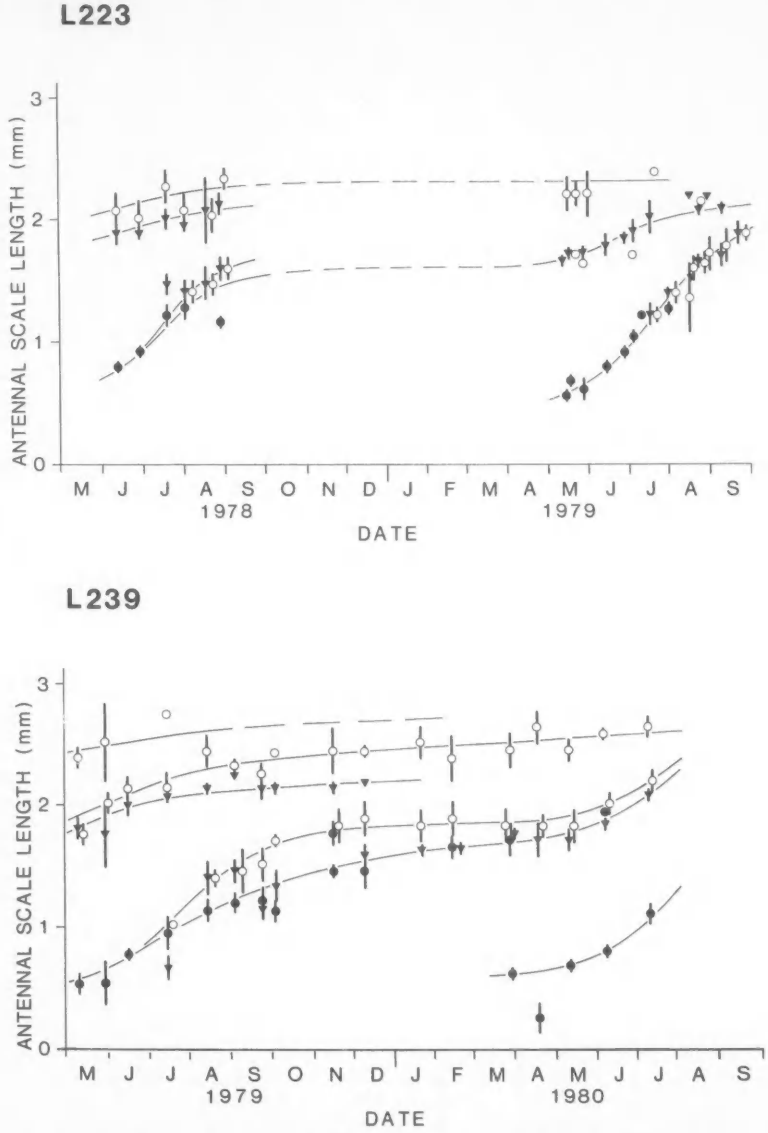

FIG. 2. Growth curves for L223 and L239 *Mysis relicta*. Eye-fitted curves have been drawn through the various cohorts and are shown as broken lines where curves have been extrapolated. Open circles denote females, triangles males, and closed circles undifferentiated females and males. Bars indicate ±95% confidence intervals.

disappearance. Growth patterns of the cohorts in L223 during the summers of 1978 and 1979 were similar to those of L239 (Fig. 2). *Mysis* growth in both lakes reached a maximum during July for the 2 yr of study. Expressed as the increase in antennal scale length per month, L223 mysids grew 0.41 mm in July 1978 and 0.40 mm in July 1979. L239 mysids grew

TABLE 2. Ranges of the mean whole body concentrations of metals in *Mysis* populations in six ELA lakes. Values of $P \leq 0.05$ indicate a significant difference between the means. The mean values have been arranged on the basis of the mean concentrations of each metal in *Mysis* samples. Values for L223 are indicated by *. Lakes for which the metal content of *Mysis* are not significantly different (Duncan's multiple range test) are represented by underscoring.

Metal	P	Order of mean metal concentrations (μg/g dry weight) Low - - - High					
Al	0.0024	46.3*	47.1	66.7	78.9	96.3	107.4
Mn	>0.05	37.4	37.9*	61.3	61.6	62.3	64.9
Fe	0.0085	89.0	111.4	119.3	194.3*	245.7	330.0
Ni	>0.05	0.50*	0.60	0.61	1.01	—	—
Cu	>0.05	43.4	44.7	58.1*	60.7	—	—
Zn	0.0002	49.7*	70.0	81.9	88.6	89.6	92.9
Cd	0.0001	0.129*	0.214	0.214	0.243	0.400	0.514
Hg	0.0001	0.151	0.349	0.379*	0.511	0.537	0.684

0.30 mm for both July 1979 and July 1980. *Mysis* in Lakes 224, 228, and 305 had lower maximum summer growth rates, ranging from 0.20 to 0.22 mm per month.

In L223 the mean antennal scale length at onset of sexual maturity for mature females of age 1+ yr was 2.24 mm. This value is significantly lower than the means (2.37−2.54) for females of the same age during similar seasons for four ELA reference lakes (Duncan's multiple range test, $P < 0.05$).

Because L223 was not sampled for *Mysis* during the winter of 1978−79, no information is available on the condition of the mysids during this period. Only one gravid female was obtained in spring 1979. This animal's brood appeared as a whitish mass, possibly a resorptive condition (Reynolds and DeGraeve 1972).

Significant differences ($P < 0.0085$) were found for the mean concentrations of Al, Fe, Zn, Cd, and Hg in the *Mysis* samples from the six lakes. For those metals that were significantly different, Duncan's multiple range test was used to determine the order of mean concentrations for the lakes. L223 *Mysis* had lower mean concentrations of Al, Zn, and Cd than any of the other five lakes (Table 2). For Hg and Fe, L223 animals had lower concentrations than animals from three and two other lakes, respectively. The storage time of the sample had no significant effect on the mean concentrations of the metals in the *Mysis* ($P = 0.11$ to $P = 0.98$).

Discussion

pH TOLERANCE OF *MYSIS RELICTA*

The 96% decrease in the *Mysis* population of L223 between August 1978 and August 1979 coincided with a 0.3 unit average decrease in the pH encountered within the water column inhabited by *Mysis*. Tests of the sampling efficiency of the net and sampling program (Nero and Davies 1982) indicated that the change in L223 population was real and could not be attributed to natural population fluctuations which, at most, result in a 50% decrease between years (Hakala 1978).

The exact pH at which the population became stressed is difficult to assess because the water column inhabited by *Mysis* often exhibited a range of pH values. The greatest pH range was during the winter when the major population decline occurred (Fig. 1). However, low numbers of adults in the population in 1978 may indicate adult *Mysis* had already declined during the winter of 1977−78 when experiencing pH values of 5.89 and lower. At pH 5.64 and lower, 96% of the 1978 population was eliminated. As mentioned above, the final 4% of the *Mysis* population died in the fall of 1979, when the pH of the zone inhabited by *Mysis* decreased suddenly from a uniform 6.2 to 5.7 (Fig. 1). This occurred during fall turnover, when acidic surface water was mixed with that in the zone inhabited by *Mysis*. Therefore, we are only able to conclude that the major *Mysis* mortality occurred at pH values between 5.9 and 5.6.

The disappearance of *Mysis* at these pH values agrees with the results obtained in Sweden (W. Dickson, Nat. Swedish Environ. Protect. Bd., Solna, personal communication; and Fürst 1981). Introductions into Ostra Nedsjon and other Swedish lakes with pH values between 5.5 and 6.1 were not successful. For example, in Lake Olen, at pH 5.1 to 6.4, *Mysis relicta* were lost, and in Lake Unden, at pH 5.9 to 6.2 the population of *Mysis* has decreased. *Mysis* introductions have been successful in lakes with pH values which remain above 6.0.

Data on pH ranges for natural and introduced populations of *Mysis relicta* in North America indicate that they can survive in lakes with pH values as low as 5.7. Dadswell (1974) found *Mysis relicta* present in lakes with a pH of 5.7, but the species was rare in lakes with such a low pH, and populations in such lakes may have been reduced by acidification (M. Dadswell, Dep. Fish. and Oceans, St. Andrews, N.B., personal communications). In a mountain lake in Wyoming, with a pH range of 5.80 to 6.90, introduced *Mysis* are well established (J. Grabowski, Wat. Res. Inst., Laramie, WY, personal communication). The above statements all suggest that *Mysis* require pH values of 5.7−5.9 or greater.

In Norway, the absence of *Gammarus lacustris* and several species of molluscs is regarded as an indicator of early damage due to acidification (Okland and Okland 1980). *Mysis relicta*, which appears to be equally sensitive, may be an early indicator of acidification in eastern Canada, where it is

widespread (Dadswell 1974).

Possible Mechanisms

The mechanism by which the *Mysis* were affected is not clear, but some possibilities can be considered. Young-of-the-year *Mysis* were collected in summer, 1979, and most of the 1978 year-class was absent in 1979, after the major decline had occurred, suggesting that reproductive failure was not the cause. Growth rate was near the upper end of the range measured in lakes in the area, which would not be expected if calcium uptake and molting were inhibited (Borgstrom and Hendrey 1976; Malley 1980). High growth rates and small size at maturity of *Mysis* in L223 could be attributed to both the oxygen and thermal regimes of L223, as well as to its higher productivity. There was no evidence of decreased zooplankton to serve as food for *Mysis* (Malley et al. 1982); indeed detailed analyses by F. DeNoyelles et al. (Dep. Ecology and Systematics, University of Kansas, Lawrence, KS, personal communication) indicate that large *Daphnia* were abundant in the zone inhabited by *Mysis*.

Increased metal concentrations in the lake cannot be implicated. As a result of the experimental acidification of L223, concentrations of Zn, Al, and Mn in the oxic water column of L223 increased only slightly (Schindler and Turner 1982). The volume weighted average concentrations of Zn rose from 2 $\mu g \cdot L^{-1}$ in 1976 to 4 $\mu g \cdot L^{-1}$ in 1979. Al concentrations increased from 8 $\mu g \cdot L^{-1}$ in 1976 to 20 $\mu g \cdot L^{-1}$ in 1979. Mn increased from 15 $\mu g \cdot L^{-1}$ in 1976 to about 90 $\mu g \cdot L^{-1}$ in 1979. Concentrations of Cd, Cu, Cr, Pb, and Co were usually below the limits of detection (<1 $\mu g \cdot L^{-1}$; Schindler et al. 1980; and unpublished data), similar to those in unacidified L224. Median concentrations in control Lake 224 were: Zn 3 $\mu g \cdot L^{-1}$, Al 15 $\mu g \cdot L^{-1}$, and Mn 6 $\mu g \cdot L^{-1}$ (Schindler et al., unpublished data).

Light transmission in the water column has increased during acidification (Schindler and Turner 1982). Smith (1970) found that light intensities of over 646 lx caused mortalities of *Mysis* in aquaria. However, the major decline in *Mysis* occurred during winter, when light intensities are well below 10 lx. Furthermore, *Mysis* in lakes 224 and 305 are abundant in areas where light intensities exceed 2000 lx.

The increased light might also have rendered *Mysis* more susceptible to predation by fish, but no increased growth of lake trout or slimy sculpins was observed (K. Mills, Dep. Fish. and Oceans, Winnipeg, Man., personal communication), as one might expect if they had eaten 96% of the *Mysis* in the lake in a few months. No other species of fish in the lake are likely to affect *Mysis* populations significantly.

Overall, direct toxicity of hydrogen ion to adult and juvenile animals appears to be the most plausible mechanism responsible for the disappearance of *Mysis*.

Our results indicate that *Mysis relicta* is one of the freshwater organisms most sensitive to pH change in North America. Its changes upon experimental acidification suggest that its tolerance is similar to the benthic crustaceans *Gammarus* and *Asellus* in Scandinavia, and to some of the most sensitive species of Mollusca (Okland and Okland 1980). In North America, only the fathead minnow *Pimephales promelas* is known to be as intolerant of low pH (Schindler 1980; Mills 1982). Because there are no body parts which are well-preserved in lake sediments (Tracy and Vallentyne 1969), there is no way of determining whether *Mysis relicta* is absent from acidified lakes which were once inhabited by the species. On the other hand, likely natural distribution patterns can be deduced with some degree of certainty from patterns of glaciation coupled with lake morphometry, temperature and oxygen data, and it seems likely that the absence of the species from suitable habitat could be regarded as an early indicator of biological damage to freshwater lakes.

Acknowledgments

We thank S. Prychitko for assistance during the night sampling. M. J. Dadswell, W. D. Dickson, and J. Grabowski kindly provided unpublished data on the pH ranges of *Mysis* populations. Mr Andy Lutz supervised analysis of *Mysis* for trace metals. P. Campbell, R. Clarke, I. J. Davies, S. Elliott, W. Franzin, J. Klaverkamp, K. Patalas, and W. G. Sprules provided constructive criticisms of the manuscript. This work was supported by a NSERC scholarship to R. W. Nero, and by the Canadian Dep. of Fisheries and Oceans.

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Zooplankton Community Structure in the North Sea and Northeast Atlantic: Development and Test of a Biological Model

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KOSLOW, J. A. 1983. Zooplankton community structure in the North Sea and Northeast Atlantic: Development and test of a biological model. Can. J. Fish. Aquat. Sci. 40: 1912–1924.

A simulation model was used to examine whether predatory interactions may regulate the size structure of marine zooplankton communities, as observed in many freshwater systems. Results of the model were consistent with the freshwater studies, such that large increases or decreases in planktivorous fish led to the dominance of small or large zooplankters, respectively. However, model predictions were not consistent with the recent decline in the northeastern Atlantic of most major elements of the pelagic zooplankton community along with North Sea herring and mackerel stocks. The overall decline of the pelagic community throughout this region indicates that zooplankton abundance may be regulated by physical forcing, and that these populations may be food- rather than predator-limited. Realistic ecological simulations of marine pelagic systems may require more complex two-layer models allowing for the effects of vertical migration, and with day–night differences in food availability and selectivity.

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Nous avons utilisé un modèle de simulation dans le but de déterminer si les interactions prédatrices peuvent régler la structure par taille des communautés zooplanctoniques marines, comme c'est le cas dans plusieurs systèmes d'eau douce. Les résultats du modèle s'accordent avec les études en eau douce, au point que de fortes augmentations ou diminutions du nombre de poissons planctivores conduisent à la dominance de petits ou de gros zooplanctontes respectivement. Cependant, les prédictions du modèle contredisent le déclin récent dans l'Atlantique nord-est des éléments les plus importants de la communauté zooplanctonique pélagique en même temps que celui des stocks de harengs et de maquereaux de la mer du Nord. Le déclin général de la communauté pélagique dans toute cette région indique que l'abondance du zooplancton peut être réglée par forçage physique, et que ces populations sont possiblement limitées par la nourriture plutôt que par les prédateurs. Des simulations écologiques réalistes de systèmes pélagiques marins peuvent nécessiter des modèles à deux couches complexes tenant compte des effets de la migration verticale et avec différences nycthémérales d'accessibilité et de sélection de la nourriture.

Received November 4, 1982
Accepted July 14, 1983

Reçu le 4 novembre 1982
Accepté le 14 juillet 1983

To what extent are marine zooplankton communities regulated by predation acting from the top down or by food limitation affecting the community from the bottom up?

Plankton-feeding fish have been found to regulate zooplankton community structure in freshwater systems in boreal and alpine regions (O'Brien 1975), in the temperate zone (Brooks and Dodson 1965; Hutchinson 1971), and in the tropics (Zaret 1972). Laboratory and field studies have shown planktivorous fish to feed size-selectively (Werner and Hall 1974; Koslow 1981), preying most heavily upon large herbivorous plankton and invertebrate predators, which in turn tend to prey upon smaller plankton. As a result of these predatory interactions, many aquatic systems with planktivorous fish tend to be dominated by small herbivorous plankton, whereas large herbivorous plankton and large planktonic predators dominate other systems without populations of plankton-feeding fish. The applicability of this paradigm to larger (Roff et al. 1981) or more productive systems (Gliwicz and Prejs 1977; Dodson 1979) has been questioned, however, and its relevance to marine systems is not known.

Coastal systems typically support large populations of plankton-feeding clupeoids and scombroids, which have been estimated to consume half or more of these systems' secondary production (Lasker 1970; Steele 1974; Koslow 1981). However, the relative importance of predation as opposed to food-limitation and competition in regulating marine zooplankton communities has been actively debated (Steele 1974;

Printed in Canada (J7109)
Imprimé au Canada (J7109)

Landry 1976; Steele and Frost 1977).

As a formal synthesis of one's understanding of a system, a model generates hypotheses by which this understanding can be tested. The model presented here focuses upon the structure of a marine-based zooplankton community consisting of a large and small herbivore and an invertebrate predator; levels of primary production and the standing stock of plankton-feeding fish are the major forcing functions. Competitive interactions between the herbivores are minimized in order to focus upon the influence of fish predation. Results of the model are examined first in relation to the freshwater paradigm and then to the changes recently recorded for pelagic communities in the North Sea and Northeast Atlantic.

The North Sea has recently been subject to a natural experiment whereby overfishing has severely reduced stocks of the dominant pelagic fish, Atlantic herring (*Clupea harengus harengus*) and Atlantic mackerel (*Scomber scombrus*). In the period 1965–70, the biomass of these species was reduced by 75% in the North Sea (Hamre 1978; Saville and Bailey 1980). This marine system and the adjacent Northeast Atlantic are unique in having been systematically surveyed during this period for the abundance of the dominant zooplankton species. I examine here the relationship between the reduction in pelagic fish biomass and the abundance of large and small predominantly herbivorous plankton and the chaetognath predator, *Sagitta* spp., in the North Sea. The changes of these zooplankters in the adjacent Northeast Atlantic serve as a control: the continental shelf west of Scotland and Ireland is relatively narrow, limiting the extent of commercial fish populations and their fisheries (Gordon and Silva 1980), so zooplankton in the Northeast Atlantic presumably did not experience a similar release in predatory pressure in the 1960s.

Methods

The development of the model is presented below, followed by the methods used to analyze the plankton data from the North Sea and Northeast Atlantic.

Components and Structure of the Model

The equations governing the model are set forth in Table 1 and a flow diagram of the program is shown in Fig. 1. All populations were assumed to be randomly distributed over a 50 m water column, which was used in all calculations of productivity or standing stocks. The smallest temporal unit used for each iteration was a day. Simulations were run for 100 and 300 d to observe the relative stability of the results.

Primary production was incorporated into the model through the carrying capacity (K_H) of the herbivorous plankton. K_H varied between 25 and 200 mg $C \cdot m^{-3}$, corresponding to primary productivity levels of approximately 0.2–2.0 g $C \cdot m^{-2} \cdot d^{-1}$, calculated from secondary production (i.e. growth + reproduction) at equilibrium and assuming 15% ecological efficiency between primary and secondary productivity.

The model contains size-structured populations of large and small herbivorous zooplankters based upon data for *Calanus* spp. (Mullin and Brooks 1970; Steele 1974; Steele and Frost 1977) and the small copepods, *Paracalanus parvus* (Checkley 1980) and *Acartia clausi* (Durbin and Durbin 1978; Landry 1978a). The body weight of individuals in each successive size-class in the model increases by 0.5 log units, small herbivores ranging from 0.02 to 20 μg C and large herbivores from 0.10 to 100 μg C.

During each iteration (day), secondary production is determined from the discrete form of the logistic equation (Eq. 1, Table 1). The small herbivore maintains isochronal growth as noted for small copepods by Miller et al. (1977) and McLaren (1978). Growth rate in the large herbivore declines with increasing body size (Marshall and Orr 1955; Mullin and Brooks 1970; Paffenhofer 1976). The minimum generation time for the small herbivore was 20 d ($k = 0.26$) (Marshall 1949; Landry 1975) and for the large herbivore was 30 d (k declines from 0.35 for the first stage to 0.11 for the egg-laying rate of the adult female) (Marshall et al. 1934; Paffenhofer 1970, 1976). Since growth in all herbivore size-classes is limited by a single logistic term, there is no niche separation between the different herbivore compartments in the model, consistent with the findings of Poulet (1978).

The size range of the invertebrate predators (0.10–100 μg C) corresponds to chaetognaths 1–11 mm in length (calculated from Sameoto (1971)). During each iteration of the model, the predators in each size-class search a particular volume of water (VSC) and extract prey within a particular size-range (F_{min}–F_{max}) up to a maximum ration size (R_{max}). Each of these latter three parameters is a function of the predator's size (Eq. 4–7, Table 1) based upon studies of predatory copepods (Landry 1978b; Lampitt 1978) and chaetognaths (Feigenbaum and Reeve 1977; Reeve and Walter 1972; Pearre 1980). The sensitivity of the model was examined over a two-fold range of search capabilities ($a = 25$–50; unless otherwise specified, $a = 37.5$; Eq. 4, Table 1). The largest prey consumed by the adult carnivores are adult small herbivores and early copepodites of the large herbivore. Thus predation by the planktonic carnivore falls most heavily on the small herbivore population, and the later stages of the large herbivore population escape. Minimum prey size was set at 10% maximum prey size (Eq. 6, Table 1).

All growth and reproduction in the invertebrate carnivores is based on the mass balance equation $P = AR - T$ (Eq. 2, Table 1), where P = production, A = assimilation efficiency, R = ration, and T = metabolic costs. Maximum daily ration of the adult invertebrate carnivore is 10% of its body weight and 75% of the body weight of stage 1 carnivores (Eq. 7, Table 1) (Reeve and Walter 1972). Assimilation efficiency varies between $A = 0.7$ at $R = R_{max}$, and $A = 0.9$ at maintenance ration levels (Eq. 3, Table 1). The weight-dependent function for metabolism is based upon general studies of zooplankton metabolism by Ikeda (1970) and Sushchenya (1970) (Eq. 8, Table 1). Active metabolism, when $R = R_{max}$, is twice the metabolic rate when no prey are available ($R = 0$). Gross growth efficiency for the invertebrate predators varies at R_{max} from 37% for the early stages to 21% for the adults, similar to growth efficiencies observed for zooplankton populations raised in culture (Mullin and Brooks 1970; Paffenhofer 1976).

All mortality in the invertebrate predators, other than that due to weight-loss when $AR - T < 0$, results from predation

TABLE 1. Equations and parameters.

Herbivores

Growth and reproduction: $$N_{i_{t+1}} = N_{i_t} + \frac{(k_{i-1})\,(L)\,(W_{i-1})\,(N_{i-1_t})}{W_i - W_{i-1}} - \frac{(k_i)\,(L)\,(W_i)\,(N_{i_t})}{W_{i+1} - W_i} \quad (1)$$

Where N = Number in a size-class
W = Weight of members of that size-class
k = Coefficient of maximal growth of a size-class
$L = \frac{K_H - \Sigma H}{K_H}$, where K_H = Herbivore carrying capacity (25−200)
ΣH = Total herbivore biomass

Invertebrate carnivores

Production: $P = AR - T$

R = Ration
T = Metabolism (2)

Assimilation:

$$A = \frac{0.41W^{0.65} - 0.09W^{0.75} - 0.18R}{0.45W^{0.65} - 0.12W^{0.75}} \quad (3)$$

W = weight of carnivore

Volume swept clear: $\mathrm{VSC} = aW^{0.85}$ (4)

(a = 25−50)

Maximum prey size: $F_{max} = 0.07\ W^{0.85}$ (5)

Minimum prey size: $F_{min} = 0.10\ F_{max}$ (6)

Maximum ration: $R_{max} = 0.50\ W^{0.85}$ (7)

Metabolism: $T = 0.15\ W^{0.75}\ (\mathrm{EXP}\ (0.69\ (R - R_{max})/R_{max}))$ (8)

Fish

Density: 3.3−330 mg C/m^3

Slope of feeding selectivity: Slope = 0.7 (1/ω) + 0.03 (9)

ω = range of prey sizes

Fraction consumed of prey$_i$: FC = ((Prey size) × (Slope)) × (Fraction space searched) (10)

R_{max} = 1.25 − 10% B.W./Day

Fraction of volume searched: $FS = 0.20\ (1 - \mathrm{EXP}\ (2.1 \times 10^{-2} \times \text{Fish density}))$ (11)

by larger invertebrate predators and planktivorous fish.

The fish component of the model contains no size or age structure. The standing stock of fish varies in the model by two orders of magnitude (3.3−330 mg C·m^{-3} = 3.3−300 t wet wt·km^{-2} assuming a 5% conversion from wet weight to carbon and restriction to a 50 m water column). This reflects biomass levels and variability noted for clupeoids in historic and recent geologic records in the California and Peruvian upwelling systems (Smith 1972; Soutar and Isaacs 1974; Schaefer 1970) and in the North Sea (Anderson and Ursin 1977). The standing stock of fish is constant during a simulation, consistent with the fish's longer generation time relative to the zooplankton.

Estimation of the fraction of the volume searched daily was based upon literature values for the schooling characteristics of the northern anchovy, *Engraulis mordax*. A 33 t school was assumed to forage in the upper 50 m within a square km (Smith 1972; Hewitt et al. 1976). Given a packing density of 100 fish·m^{-3} (100 g C·m^{-3}) (Graves 1977), an elongate cylindrical school (5 m radius and 211 m in length) could

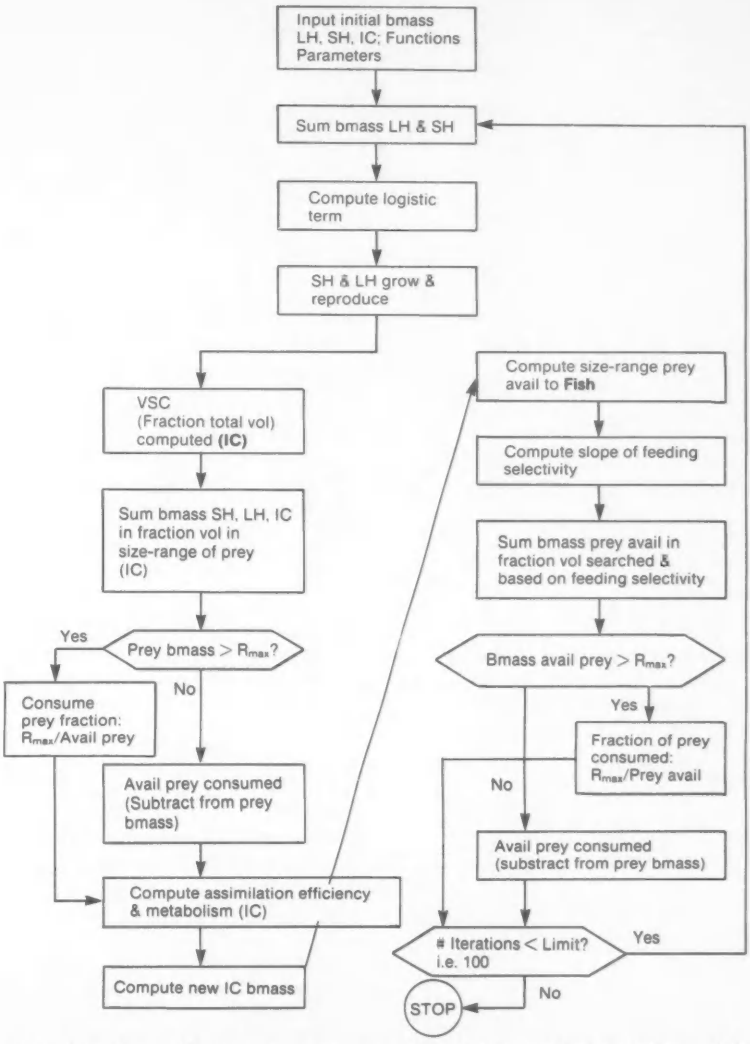
Input initial bmass LH, SH, IC; Functions Parameters
Sum bmass LH & SH
Compute logistic term
SH & LH grow & reproduce
VSC (Fraction total vol) computed (IC)
Sum bmass SH, LH, IC in fraction vol in size-range of prey (IC)
Yes
Prey bmass > Rmax?
No
Consume prey fraction: Rmax/Avail prey
Avail prey consumed (Subtract from prey bmass)
Compute assimilation efficiency & metabolism (IC)
Compute new IC bmass
Compute size-range prey avail to Fish
Compute slope of feeding selectivity
Sum bmass prey avail in fraction vol searched & based on feeding selectivity
Bmass avail prey > Rmax?
Yes
Fraction of prey consumed: Rmax/Prey avail
No
Avail prey consumed (substract from prey bmass)
Iterations < Limit? i.e. 100
Yes
No
STOP

FIG. 1. Flow diagram of the computer program governing the simulation model of large herbivores (LH), small herbivores (SH), invertebrate carnivores (IC), and fish.

cover approximately 15% of the volume in 10 h if foraging continuously at 1 body length·s^{-1} (10 cm·s^{-1}). The model was examined for its sensitivity to changes in the fraction of the volume searched daily over a four-fold range (5–20%), and the fraction of the volume searched was made a function of fish density and varied within this range (Eq. 11, Table 1). Feeding is size-selective, such that a maximum of 100% of the largest prey and 15% of the smallest prey are consumed (Koslow 1981). Consumption of smaller plankton is a decreasing linear function of prey size, and the slope of this function varies in relation to the size range of prey available (Eq. 9, Table 1) (Koslow 1981). In computing the size-range of available prey, a size-category of prey is assumed present only if in numbers greater than 1·m^{-3} for large herbivores and predatory plankton and 10·m^{-3} for the small herbivores. Maximum daily ration size (R_{max}) was set at 5% of body weight.

In summary, at each iteration the large and small herbivores grow and reproduce based upon a single discrete form of the logistic function (Fig. 1). The planktonic predators then prey

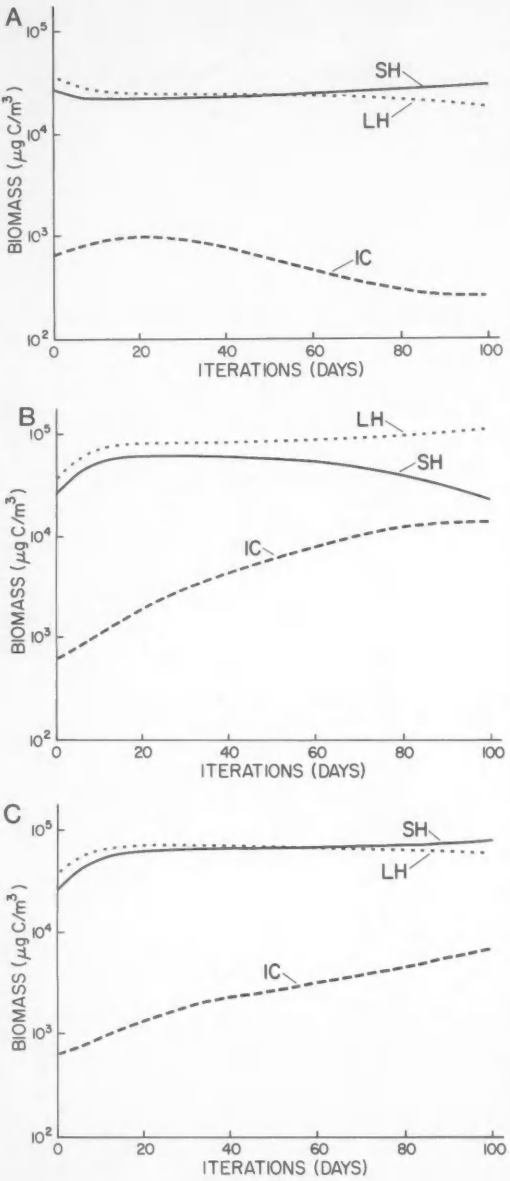

FIG. 2. The biomass (μg $C \cdot m^{-3}$) of large herbivores (LH), small herbivores (SH), and invertebrate carnivores (IC) in three computer simulations, in which only the herbivore carrying capacity (K_H) (= primary productivity) and standing stock of planktivorous fish were varied. (A) K_H = 50 mg $C \cdot m^{-3}$ = 0.5 g $C \cdot m^{-2} \cdot d^{-1}$ primary production; fish = 33 mg $C \cdot m^{-3}$; (B) K_H = 150 mg $C \cdot m^{-3}$; fish = 33 mg $C \cdot m^{-3}$; (C) K_H = 150 mg $C \cdot m^{-3}$; fish = 60 mg $C \cdot m^{-3}$.

upon smaller invertebrates and grow and reproduce in relation to the amount of prey they consume. The invertebrate populations are then preyed upon size-selectively by the fish. The response of the model was examined in relation to (1) changes in primary productivity, incorporated in the herbivores' carrying capacity (K_H); and (2) changes in the standing stock of fish. The sensitivity of the model was also analyzed in relation to parameters characterizing the feeding of the fish, invertebrate predators and herbivores.

North Sea and Northeast Atlantic Plankton Data

Details of the Continuous Plankton Recorder (CPR) survey and data processing are presented in Glover (1967) and Colebrook (1960, 1975). Data from the CPR survey are available as the log-transformed abundance of major plankton species reported for standard areas. North Sea herring data for 1950–76 (Saville and Bailey 1980), and monthly zooplankton data (1948–80), and phytoplankton data (1958–80) were used in this study. The plankton data from the CPR survey were kindly made available by the Institute for Marine Environmental Research, Plymouth, U.K. It should be noted that due to the standard mesh size of the CPR (0.27 mm), small zooplankters and most phytoplankton are inadequately sampled.

The numerical abundance of each zooplankton species was multiplied by the adult weight of the species (Mullin and Brooks 1970; Steele and Frost 1977; Miller et al. 1977; Durbin and Durbin 1978; Checkley 1980) to form an index of biomass. The biomass of the large copepods *Calanus helgolandicus* and *C. finmarchicus* were added to form a composite index for the large herbivores; data for the small copepods *Paracalanus parvus*, *Pseudocalanus* spp., and *Acartia* spp. were similarly combined as an index for the small herbivores; and data for the invertebrate predator, *Sagitta* spp., were similarly transformed. The time series for sixteen diatom species groups (*Paralia sulcata*, *Skeletonema costatum*, *Thalassiosira* spp., *Dactyliosolen mediterraneus*, five species of *Rhizosolenia*, *Hyalochaete* spp., *Phaeoceros* spp., *Asterionella japonica*, *Thalassiothrix longissima*, *Thalassionema nitzschioides*, *Nitzschia seriata*, and *N. delicatissima*) were added to form an index of diatom abundance; and seven species of the dinoflagellate, *Ceratium* spp., were added to form an index of this group. Abundance indices for large and small herbivores, invertebrate predators, diatoms, and the dinoflagellate, *Ceratium* spp., were thus obtained for each standard area of the CPR survey. To obtain monthly indices over wider areas — namely the North Sea and Northeast Atlantic — the arithmetic mean was taken by month for each planktonic group over the six standard sampling areas of the North Sea (B1-2, C1-2, D1-2: approximately 51°–61°N, 8°E–3°W) and six areas of the Northeast Atlantic west of Britain (B4-5, C4-5, D4-5: approximately 50°–63°N, 3°–19°W (Glover 1967; Colebrook 1960, 1975)). Because the index values for the standard areas within the North Sea or Northeast Atlantic were highly intercorrelated, regional means were predicted when there were missing values using a least-squares estimate based upon the relation between the missing and non-missing values in the rest of the data set (for derivation, see Chelton et al. 1982). The expected error of the estimate can also be determined, and the regional mean was

treated as missing if the estimated error was greater than 25%.

Since the interannual rather than the seasonal plankton dynamics were of interest, the seasonal cycle was removed from the data by taking a 13-mo running mean of the data. Standard correlation and regression analyses were then performed on the deseasonalized time-series.

In determining the significance of all correlations, the degrees of freedom were corrected for autocorrelation in the data using C. Garrett's (Oceanogrpahy Dep., Dalhousie Univ., personal communication) modification of the method of Davis (1977).

The combined biomass of the three major North Sea herring stocks, which mix when they feed in the central North Sea, was used as the index of planktivorous fish (Saville and Bailey 1980). Herring have been the dominant feeder on copepods in the North Sea, at least for most of the study period (Steele 1974), and it is the only planktivorous fish species for which there is an adequate record of abundance. The trend for mackerel is similar (Hamre 1978). Herring biomass was assumed constant throughout the calendar year.

The time series were also detrended in order to analyze the data without the influence of long-term trends. A linear regression was performed on each set of data against the sample date, and residuals from the regression were used as the detrended time series.

Results

Simulation Model

The results of three typical simulations are shown in Fig. 2. At moderately high levels of primary productivity (K_H = 50 mg C·m^{-3} = 1.0–1.5 g C·m^{-2}·d^{-1} primary production) and fish (33 mg C·m^{-3}), large and small herbivores were approximately equally abundant (Fig. 2A). The relative dominance of the large herbivores increased when the productivity of the system was substantially increased (Fig. 2B) and vice-versa. The dominance of the large herbivores was inversely related to the density of planktivorous fish (see Fig. 2C, where fish density is approximately doubled, other parameters as in Fig. 2B).

The response of the zooplankton populations was examined at the end of 100-d simulations to seven levels of fish density and four of herbivore carrying capacity (Fig. 3). The planktivorous fish were negatively correlated with their principal prey items, the large herbivores and invertebrate predators, and strongly positively correlated with the small herbivores (Table 2), due to the inverse relationship between the small herbivores and both their competitor (the large herbivores) and major predator (the invertebrate carnivore). The large herbivores were significantly positively correlated with primary productivity. However, the small herbivores showed no significant relationship with primary production because at low-to-moderate densities of fish, the small herbivores were

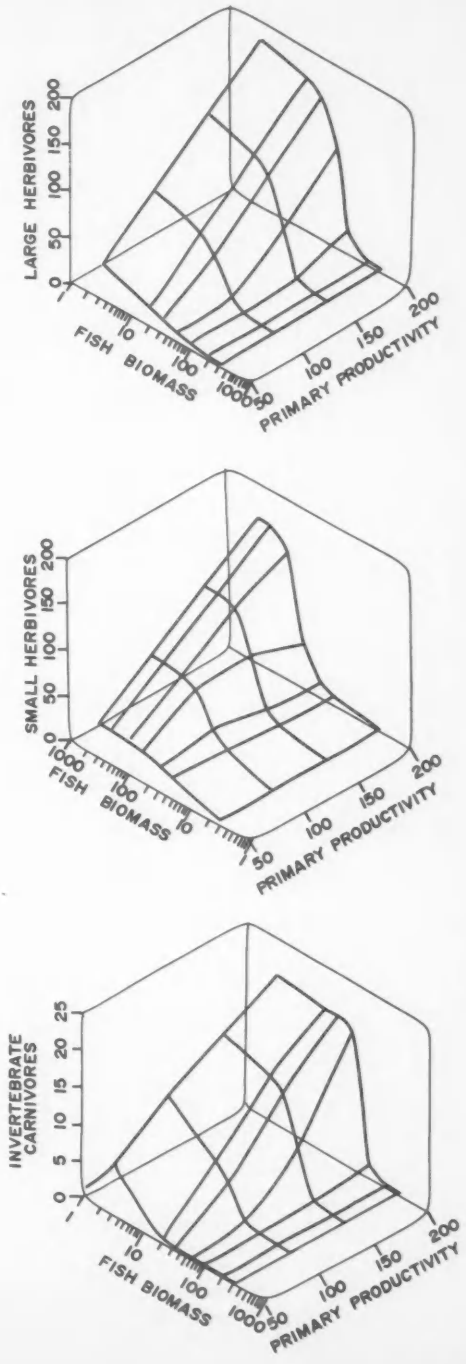

FIG. 3. The biomass (mg C·m^{-3}) of large and small herbivores and invertebrate carnivores at the end of 100-d simulations in response to several levels of fish stock biomass (mg C·m^{-3}) and primary productivity (= herbivore carrying capacity (K_H)) (mg C·m^{-3}). Note that the scale for fish biomass in the figure for small herbivores is reversed from that in the other figures.

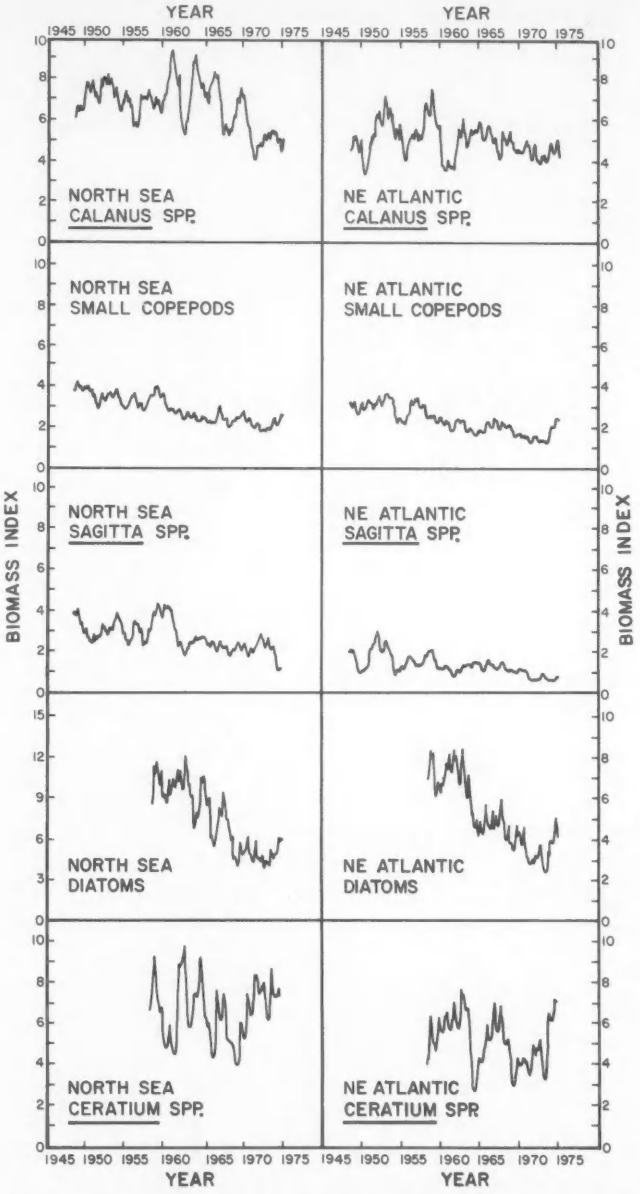

FIG. 4. Time series based upon the biomass of plankton groups averaged over the North Sea and Northeast Atlantic: large herbivorous copepods (*Calanus* spp.), small herbivorous copepods, invertebrate predators (*Sagitta* spp.), diatoms, and dinoflagellates (*Ceratium* spp.). The seasonal cycle was removed from the monthly data using a 13-mo running mean.

TABLE 2. Spearman's ρ correlations between fish biomass, zooplankton carrying capacity (K_H), large and small herbivorous plankton, and invertebrate carnivores. Data are results of the simulation model after 100 iterations (= days). Significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Fish	Large herbivores	Small herbivores	Invertebrate carnivores
K_H	0.00	0.51*	0.08	0.70***
Fish		−0.81***	0.92***	−0.61**
Large herbivores			−0.74***	0.90***
Small herbivores				−0.55**

TABLE 3. Product moment correlation coefficients between the biomass of North Sea herring (2-yr and older) (1950−76) and the deseasonalized monthly time series of the biomass of the large herbivore, *Calanus* spp., small herbivorous copepods, the invertebrate carnivore, *Sagitta* spp. (1948−80), and of diatoms and the dinoflagellate, *Ceratium* spp. (1958−80), in the North Sea. Significance levels (df) are corrected for serial correlation (see text). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ (tests 2-tailed).

	Small copepods	*Sagitta*	Diatoms	*Ceratium*	Herring
Calanus	0.44*	0.55***	0.52**	−0.13	0.74**
	(28)	(31)	(30)	(29)	(11)
Small copepods		0.72***	0.71**	0.39	0.66*
		(24)	(13)	(23)	(11)
Sagitta			0.63*	0.37	0.65**
			(9)	(21)	(16)
Diatoms				0.44**	0.83***
				(31)	(31)
Ceratium					0.06
					(30)

buffered from the effects of changes in primary productivity by concomitant changes in the large herbivores and invertebrate predators. The large herbivores were not similarly buffered because the biomass of their major predator, the planktivorous fish, was fixed during the course of each simulation because of their longer generation time. As a result of these interactions, the large herbivores and invertebrate predator were positively correlated. There were no significant differences between the results of simulations conducted for 100 and 300 d. In general, these results are consistent with observations of zooplankton community structure in freshwater systems (Brooks and Dodson 1965; Hutchinson 1971; Zaret 1972; O'Brien 1975), although the relationship between primary production and zooplankton community structure was not explicitly addressed in most freshwater studies.

North Atlantic Plankton

The deseasonalized time series for the large and small herbivorous copepods, chaetognaths, diatoms and herring in the North Sea and Northeast Atlantic all declined during the period 1950−75 (Fig. 4). The correlation matrix for the North Sea pelagic community (Table 3) indicates strong positive correlations among the time series of all groups with the exception of *Ceratium* spp., which showed no significant decline during this period. The direction of most of these correlations is opposite to that predicted by the predation-based model, insofar as the model predicted negative correlations between (1) the large and small herbivorous competitors, (2) the planktonic predator and its small planktonic prey, and (3) the herring and both *Calanus* spp. and *Sagitta* spp. Although the model predicted a positive correlation between *Calanus* spp. and diatom production, it did not predict the strong correlation found between small herbivorous copepods and diatom abundance.

A similar pattern was found in the data for the Northeast Atlantic planktonic community (Table 4). Again, the time series of almost all planktonic groups except *Ceratium* spp., which is not significantly grazed by most herbivorous copepods, were significantly positively correlated with each other. Moreover, there were consistent strong positive correlations between the time series for the plankton in the North Sea and Northeast Atlantic with the exception of *Ceratium* spp. and in the Northeast Atlantic, of *Calanus* spp. (Table 5).

The plankton in the Northeast Atlantic showed unexpected significant correlations with the North Sea herring (Table 5). While these correlations may be spurious, they also suggest the decline of the herring may have been related not only to overfishing but to underlying ecological changes, which limited recruitment to the pelagic fisheries just as they reduced

TABLE 4. Product moment correlation coefficients between the deseasonalized monthly time series of the biomass of the large herbivore, *Calanus* spp., small herbivorous copepods, and the invertebrate carnivore, *Sagitta* spp. (1948–80), and of diatoms and the dinoflagellate, *Ceratium* spp. (1958–80) in the Northeast Atlantic plankton. Significance levels (df) are corrected for serial correlation (see text). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ (tests 2-tailed).

	Small copepods	*Sagitta*	Diatoms	*Ceratium*
Calanus	0.41* (34)	0.62*** (38)	0.24 (30)	−0.22 (42)
Small copepods		0.72*** (29)	0.79*** (19)	0.65*** (77)
Sagitta			0.59** (26)	0.02 (48)
Diatoms				0.51** (32)

plankton standing stocks over the entire northeastern Atlantic. If this were true, a stronger correlation would be expected if the herring data were lagged back to the time of spawning; if false, a weaker relationship should emerge. However, an attempt to test this hypothesis produced equivocal results. Lagging the herring data from 1 to 3 yr produced little change in the magnitude of the correlations with the plankton. While lagged correlations with *Calanus* spp. and *Sagitta* spp. were generally weaker, lagged correlations with the small herbivorous copepods and diatoms were generally stronger (Table 6).

Since any data sets exhibiting strong trends will appear correlated, it is often valuable to reexamine such relationships after detrending them. In examining the detrended time series, most elements of the Northeast Atlantic plankton remained significantly positively correlated with each other, and the sign of the correlations remained opposite to that found in the model. However, few strong correlations remained among components of the North Sea plankton or between the North Sea and Northeast Atlantic plankton. The lagged herring remained strongly correlated only with diatom abundance (correlation with 3-yr lag with North Sea diatoms: $r = 0.46$, $P < 0.05$). Contrary to model predictions, the herring continued to be positively correlated with North Sea *Calanus* spp. ($r = 0.52$, $P < 0.01$). The small copepods remained correlated with diatom abundance (North Sea: $r = 0.32$, $P < 0.05$; Northeast Atlantic: $r = 0.50$, $P < 0.01$), but correlations between *Calanus* spp. and diatoms were no longer significant.

To concentrate upon direct interactions, partial regression analysis was performed on the data. The regressions with *Sagitta* spp. were run without phytoplankton included, and those for Northeast Atlantic zooplankton were performed without herring included. The close correlations of North Sea *Calanus* spp., diatoms, and herring (Table 3) produced anomalous results when herring was included in the regression for *Calanus* spp., so this regression was performed both with and without herring included (Table 7).

The herring continued to show statistical relationships to the North Sea plankton opposite to those predicted by the model: strong positive relationships with the large plankters, *Calanus* spp. and *Sagitta* spp., and a negative relationship with the small copepods. In general, however, the large and small herbivores showed stronger relationships with the phytoplankton than with each other or with *Sagitta* spp. The abundance of the herbivorous plankton thus appears more strongly regulated by fluctuations of their food supply than by competition or predation. Differences in food preference are indicated by the consistent negative correlation between the abundance of *Calanus* spp. — but not the small copepods — and *Ceratium* spp. However, all herbivores were strongly correlated with diatom abundance with the exception of Northeast Atlantic *Calanus* spp. The multiple regressions were all highly significant and the proportion of the total variance explained ranged from 0.43 to 0.89.

TABLE 5. Product moment correlation coefficients between the biomass of North Sea herring (2-yr and older) (1950–76) and the deseasonalized monthly time series of the biomass of the large herbivore, *Calanus* spp., small herbivorous copepods, and the invertebrate carnivore, *Sagitta* spp. (1948–80), and diatoms and the dinoflagellate, *Ceratium* spp., (1958–80) in the North Sea and Northeast Atlantic plankton. Significance levels (df) are corrected for serial correlation (see text). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ (tests 2-tailed).

	Northeast Atlantic				
North Sea	*Calanus*	Small copepods	*Sagitta*	Diatoms	*Ceratium*
Calanus	0.29 (31)	0.45* (23)	0.54** (29)	0.60*** (29)	0.05 (35)
Small copepods	0.23 (38)	0.81*** (15)	0.63*** (39)	0.70** (12)	0.38*** (77)
Sagitta	0.20 (37)	0.56** (18)	0.60*** (31)	0.64* (8)	0.09 (27)
Diatoms	0.25 (30)	0.70*** (20)	0.61*** (27)	0.89*** (12)	0.40* (32)
Ceratium	0.18 (19)	0.31 (29)	0.19 (29)	0.30 (31)	0.32* (49)
Herring	0.38 (25)	0.68* (8)	0.62** (17)	0.74* (8)	0.03 (20)

TABLE 6. Product moment correlation coefficients between the North Sea herring biomass (2-yr and older) lagged 0 and 3 yr and the deseasonalized monthly time series of the biomass of the large herbivore, *Calanus* spp., small herbivorous copepods, and the invertebrate carnivore, *Sagitta* spp. (1950–76), and diatoms and the dinoflagellate, *Ceratium* spp. (1958–76) in the (a) North Sea and (b) Northeast Atlantic plankton. Significance levels (df) are corrected for serial correlation (see text). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ (tests 2-tailed).

	Calanus	Small copepods	*Sagitta*	Diatoms	*Ceratium*
			(a) *North Sea*		
Herring 0-lag	0.74** (11)	0.66** (11)	0.65** (16)	0.83*** (13)	0.06 (30)
Herring lagged 3 yr	0.45 (17)	0.79** (9)	0.57** (25)	0.85*** (10)	0.14 (24)
			(b) *Northeast Atlantic*		
Herring 0-lag	0.38 (25)	0.68* (8)	0.62** (17)	0.74* (8)	0.03 (20)
Herring lagged 3 yr	0.25 (25)	0.80** (8)	0.50* (17)	0.92*** (9)	0.47 (15)

TABLE 7. Partial regression coefficients from standard multiple regression analyses with *Calanus* spp., small herbivorous copepods, and *Sagitta* spp. in the North Sea and Northeast Atlantic as dependent variables and, as appropriate, elements of these plankton communities, North Sea herring biomass (2-yr and older), and diatom and *Ceratium* spp. as independent variables. Analysis for North Sea *Calanus* spp. is performed with (1) and without (2) North Sea herring biomass included as an independent variable. R^2 is the variance explained by the multiple regression. Significance levels (df) corrected for serial correlation based upon values from Tables 3 and 4 (see text). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Dependent variables						
	North Sea				Northeast Atlantic		
Independent variables	*Calanus* (1)	*Calanus* (2)	Small copepods	*Sagitta*	*Calanus*	Small copepods	*Sagitta*
Calanus			0.28* (24)	0.10 (29)		0.23*** (31)	0.48*** (37)
Small copepods	0.13* (24)	−0.11 (25)		0.22** (22)	0.51*** (31)		0.28*** (28)
Sagitta	−0.06 (27)	0.39*** (28)	0.50*** (20)		0.37*** (35)	0.18** (26)	
Diatoms	−0.35*** (26)	0.49*** (27)	1.01*** (9)		−0.09 (27)	0.33*** (16)	
Ceratium	−0.32*** (25)	−0.45*** (26)	−0.06 (19)		−0.43*** (39)	0.53*** (74)	
Herring	1.07*** (7)		−0.95*** (7)	0.50*** (14)			
R^2	0.78	0.60	0.53	0.52	0.42	0.74	0.40

Since the major trends in the plankton community appeared to be region-wide, it seemed advisable to remove the influence of the Northeast Atlantic plankton upon the plankton of the North Sea and to reexamine whether the decline of the North Sea herring influenced the structure of the North Sea zooplankton community. The North Sea zooplankton time series were normalized to the Northeast Atlantic by taking the ratios of the biomass of North Sea to Northeast Atlantic zooplankters (i.e. *Calanus* spp., small herbivores, and *Sagitta* spp.). There were no trends in these time series, and only *Calanus* spp. was significantly correlated with herring ($r = 0.44$, $P < 0.05$), but the sign of the correlation was again opposite to that predicted by the model.

Discussion

The results of the model appear entirely consistent with the freshwater paradigm. Large herbivores and invertebrate predators dominate when stocks of planktivorous fish are low, and small herbivores dominate when stocks of these pelagic

fish are high (Fig. 3). The model also predicts that large and small plankton may co-occur with plankton-feeding fish in non-oligotrophic systems, consistent with Gliwicz and Prejs (1977) and Dodson (1979). Thus a model based primarily upon predatory interactions appears adequate to describe much of the structural dynamics of simple planktonic communities.

However, recent changes in the pelagic community of the North Sea are entirely inconsistent with the predictions both of the present model and studies of freshwater systems. In the period 1960–70, the biomass of herring and mackerel, the dominant copepod feeders in the North Sea, declined 65% (table 24, Anderson and Ursin 1977), and the biomass of North Sea herring subsequently declined even further. Based upon this model one would predict that large herbivores and invertebrate predators would increase in this period. Instead, all major planktonic groups experienced a severe decline.

But was there in fact a significant decline in planktivorous fish in the North Sea during this period? It has been argued that increases in other planktivorous fish species (e.g. whiting (*Merlangius merlangus*), pout (*Trisopterus esmarki*), juvenile Atlantic cod (*Gadus morhua*), sandeels (*Ammodytes* spp.), and sprat (*Sprattus sprattus*)) have compensated for the decline in herring and mackerel (Anderson and Ursin 1977). Following the demise of the region's herring and mackerel stocks, the industrial fisheries shifted to nontraditional species and the level of fish landings for planktivorous fish remained approximately unchanged. While there are records of landings, there are no adequate time series of year-class strength for the nontraditional planktivores (i.e. pout, sandeels, and sprat) (Holden 1978), so it is not possible to determine how these populations varied in recent decades.

The evidence from systems in which pelagic fishery surveys are regularly conducted indicates that replacement of one fish species by another typically requires on the order of a decade or more. Replacement of sardine (*Sardinops sagax*) by anchovy (*Engraulis mordax*) in the California Current required at least 12 yr (1950–62), despite the lack of any significant fishery on the anchovy (Smith 1972). Similarly, in the Peru Current, sardine (*S. sagax*) have not fully replaced the anchovetta (*E. ringens*), which collapsed in the early 1970s and it appears that herbivorous zooplankton increased significantly during this time (Walsh et al. 1980). It therefore seems unlikely that herring and mackerel were substantially replaced in the North Sea in a decade of greatly increased fishing effort on all major planktivorous species. This is consistent with Coombs (1975), who reported a general decline of larval fish in the North Sea during the period of study. Planktivorous gadoids, such as whiting and pout, do not feed in the epipelagic zone with the herring and mackerel, but rather at 100–200 m, and their diet consists predominantly of deeper-living plankton, such as euphausiids (Raitt and Adams 1964). Young cod feed primarily upon copepods for only a brief period in their early life history (Cushing 1980).

Anderson and Ursin (1977) argue that an increase in invertebrate predators may also have compensated for the decline in herring and mackerel. However, there is no indication in the CPR data that any invertebrate predator increased during this period; indeed, euphausiids, amphipods, and chaetognaths appear to share the general decline of the other plankton groups (Colebrook 1978). Anderson and Ursin (1977) therefore argue that gelatinous zooplankton, which are not sampled by the plankton recorder, were responsible for a proposed increase in invertebrate predation. However, coelenterates and *Pleurobrachia pileus*, the only abundant North Sea ctenophore, are largely restricted to neritic waters (Fraser 1970; Moller 1980). Furthermore, the decline in amphipods (Colebrook 1978), some of which are associated with coelenterates, is inconsistent with a hypothetical increase in coelenterates. Available evidence thus indicates a general decline of invertebrate predators during the study period.

The decline in both the North Sea and Northeast Atlantic of major elements of the pelagic system suggests that large-scale physical processes are the dominant influence on the interannual variability of the system as concluded by Colebrook (1978, 1982). Correlations have been found between Gulf Stream position, temperature structure and westerly weather in the North Atlantic on the one hand, and zooplankton in the Northeast Atlantic and North Sea on the other (Colebrook 1978, 1982; Garrod and Colebrook 1978; Taylor and Stephens 1980). However, the mechanisms responsible for these relationships are not clear.

While physical factors may regulate the overall abundance of the northeastern Atlantic plankton, it is unclear why changes in North Sea planktivore populations failed to significantly influence the relative composition of the zooplankton community there. The implication is that the zooplankton are food-limited rather than predator-limited. This conclusion appears to bring into question Steele's (1974) calculation that herring alone consumed approximately half the herbivorous copepod production in the North Sea. Alternatively, aspects of the marine environment may enable marine zooplankton to avoid the predator regulation apparent in certain freshwater systems.

Differences in physical scale may lead to qualitative differences in the ecological dynamics of aquatic systems. Roff et al. (1981) found that large and small plankters may coexist regardless of the presence or absence of planktivorous fish in deeper, larger freshwater systems. Such behaviors as vertical migration out of the well-lit upper waters during daylight hours become possible in deeper systems, providing a refuge for larger plankters from visually orienting vertebrate predators. Koslow and Ota (1981) showed that seasonal changes in vertical migration of later copepodite stages of *Calanus pacificus* off southern California are consistent with a strategy of minimizing losses to planktivorous fish during less productive periods. Realistic simulations of fish-plankton interactions may require a two-layer model with day–night differences in the distribution of large zooplankton and both the distribution and feeding of the fish.

Acknowledgments

I thank M. Mullin for his encouragement. I thank A. Larson, G. Jackson, J. Roff, and an anonymous reviewer for their helpful comments. R. Hody, M. Thompson, and B. McCabe assisted with the computer. This work was supported by NSF Grant OCE76-02035, DOE Contract DE-AM03-76-SF00010, and grants from the Natural Sciences and Engineering Research Council and Department of Fisheries and Oceans of Canada.

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Population and Trophic Dynamics of Pacific hake (*Merluccius productus*)

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FRANCIS, R. C. 1983. Population and trophic dynamics of Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 40: 1925 – 1943.

This paper explores the population and trophic dynamics of the coastal stock of Pacific hake (*Merluccius productus*). In particular, the biological mechanisms of growth, mortality (natural and fishing), migration, and bioenergetics are quantified in such a way that both fishery and trophic dynamics can be explored. The central focus of the analysis is an age-structured computer simulation model. Both uniform and seasonal relationships of weight on age are derived and provide markedly different estimates of trophic demands. Variable age-specific natural mortality yields cohort analysis estimates of stock biomass which correspond more closely to survey estimates than estimates based on constant natural mortality. Bioenergetic simulations indicate that both production of and consumption by hake may be considerably lower than for other similar gadoid species. The ratio of total annual production (growth and recruitment) to biomass is estimated to be 0.35 and the average annual daily consumption is estimated to be 0.4% BWD.

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L'article qui suit contient une analyse de la dynamique de population et de nutrition du stock côtier de merlus du Pacifique (*Merluccius merluccius*). Plus particulièrement, on y quantifie les mécanismes biologiques de croissance, de mortalité (naturelle et due à la pêche), la migration et la bioénergétique, de telle façon que la pêcherie aussi bien que la dynamique trophique peuvent être explorées. L'analyse est axée sur un modèle de simulation d'ordinateur structuré par âge. On en retire des relations, tant uniformes que saisonnières, du poids à un âge donné et on obtient des estimations nettement différentes des demandes trophiques. La mortalité naturelle variable et spécifique à l'âge donne des estimations, par analyse des cohortes, de la biomasse du stock correspondant plus étroitement aux estimations des relevés que celles fondées sur une mortalité naturelle uniforme. Des simulations bioénergétiques indiquent que la production de même que la consommation chez le merlu peuvent être considérablement inférieures à ce que l'on observe chez d'autres gadoïdes semblables. On estime à 0,35 le rapport de la production annuelle totale (croissance et recrutement) à la biomasse et à 0,4 % du poids somatique la consommation quotidienne annuelle moyenne.

Received July 28, 1982
Accepted July 19, 1983

Reçu le 28 juillet 1982
Accepté le 19 juillet 1983

PACIFIC hake (also referred to as Pacific whiting), *Merluccius productus*, is commercially and ecologically one of the most important fish species on the west coast of North America. Since 1966, hake have been the target of a large foreign fishery. A small, rather insignificant, domestic fishery for hake has existed since at least 1879. Estimated catches have ranged from 91 to 236 kt annually (Bailey et al. 1982). Since 1978, U.S. and Canadian domestic joint ventures for hake have begun to develop. The U.S. joint-venture catch has been approximately 3, 13, 41, and 45 kt in 1978 through 1981.

Besides being an important resource to man, hake is also important in the California Current ecosystem. As a large predator, hake consume various quantities of other fish and shellfish populations, notably the commercially important stocks of Pacific herring (*Clupea harengus pallasi*), northern anchovy (*Engraulis mordax*), and pink shrimp (*Pandalus jordani*). Hake is also important as prey in the diets of marine mammals and large fishes (Bailey and Ainley 1982).

Bailey et al. (1982) give a detailed description of the life history of and fishery for Pacific hake. Briefly, the coastal stock of Pacific hake occupies the continental shelf and slope area of the California Current system, ranging from a feeding area off Vancouver Island in the north to a spawning area as far south as the southern tip of Baja California (Fig. 1). In autumn, adult hake migrate from the summertime feeding grounds off the Pacific Northwest to the winter spawning grounds off southern California and Baja California. In spring and summer large adult fish migrate northward as far as central Vancouver Island while juveniles remain off central and northern California. Oceanographic conditions at the time of

Printed in Canada (J7023)
Imprimé au Canada (J7023)

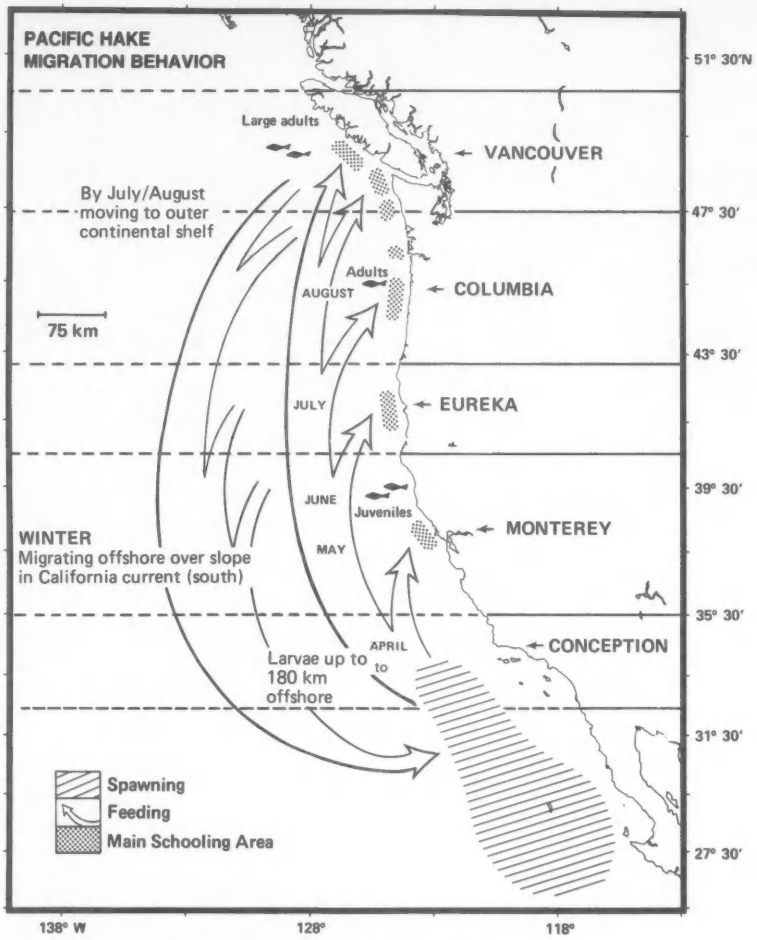

FIG. 1. Migratory patterns of Pacific hake (*Merluccius productus*).

spawning appear to play a major role in recruitment to the exploitable stock (Bailey 1981).

To aid the development of fisheries management policy, one intent of the study of the dynamics of an exploited population is to determine numbers, biomass, age (or size) structure, and potential yield. Another intent is to determine the impact the dynamics of one population might have on the production of other commercially important populations in the ecosystem. It has long been recognized (Smith 1978) that hake play an important role in the fish production of the California Current region. Although its production seems to be most heavily influenced in the southern extremes of its range (Bailey 1981; Francis et al. 1982), one might speculate that its strongest influence, as a predator and competitor, occurs during its summer feeding migrations to the north. In this paper, I estimate the impact of hake, both in an unfished and fished state, on the trophic dynamics of their northern feeding grounds. In doing so I attempt to quantify the mechanisms of growth, mortality, migration, and bioenergetics in such a way that both fishery and trophic dynamics can be explored. Ultimately what is produced is ecosystem simulation from the inside out, the inside or focus being the hake population. My hope is that the results of this analysis might help to validate or invalidate this type of approach to exploring the bioenergetics of a commercially exploited fish population.

The tangible product of this analysis is an age-structured computer simulation model, entitled HAKE. Population parameters estimated in this analysis are also subsequently used in a management analysis of the Pacific hake fishery

(Francis et al. 1982). A listing of the model code can be obtained on request from the author.

The Simulation Model

The basic structure of the simulation model (HAKE) is similar to that described by Francis (1974, 1977) and Walters (1969). Its primary function is to describe accurately variation in Pacific hake biomass over time and area. The model is dynamic and provides a tool for synthesizing, summarizing, and evaluating the processes of growth, mortality, and migration. Analysis of these processes is presented in later sections. The model may also be used to estimate stock bioenergetic demands.

The essential structural units of HAKE are the hake age-groups, quarters of a year, and International North Pacific Fisheries Commission (INPFC) statistical areas. Letting

i = age-group (2, . . . , 12),

j = area (1, . . . , 6),

$x \in [t, t+1]$ (t being in quarterly time units),

$N_{ij}(x)$ = number of fish of age i in area j at time x,

$Z_{ij}(t)$ = mean instantaneous total mortality rate on age-group i over $[t, t+1]$,

$$= F_{ij}(t) + M_i,$$

$$= q_{ij} f_j(t) + M_i,$$

$F_{ij}(t)$ = mean instantaneous fishing mortality rate on age-group i over $[t, t+1]$,

M_i = mean instantaneous natural mortality rate on age-group i,

q_{ij} = catchability coefficient on age-group i in area j,

$f_j(t)$ = number of standard days effort in area j during $[t, t+1]$,

then

$$\frac{dN_{ij}(x)}{dx} = \left[-Z_{ij}(t) - \sum_{K(\neq j)=1}^{6} I_i^{jk}(t)\right] N_{ij}(x) + \sum_{K(\neq j)=1}^{6} I_i^{kj}(t)\, N_{ik}(x)$$

where

$I_i^{jk}(t)$ = mean instantaneous migration rate of age-group i from area j to area k over $[t, t+1]$.

Also

$YN_{ij}(t)$ = catch in numbers of age-group i in area j during $[t, t+1]$

$$= \int_t^{t+1} F_{ij}(t)\, N_{ij}(x)\, dx.$$

$YW_{ij}(t)$ = catch in weight of age-group i in area j during $[t, t+1]$

$$= \int_t^{t+1} F_{ij}(t)\, B_{ij}(x)\, dx$$

$B_{ij}(x)$ = biomass of age-group i in area j at time x

$$= N_{ij}(x)\, w_i(t)\, e^{g_i(t)(x-t)},$$

$w_i(t)$ = average weight of an individual on entry into age-group i during $[t, t+1]$, and

$g_i(t)$ = instantaneous growth of age-group i during $[t, t+1]$

$$= \ln\left[\frac{w_{i+1}(t+1)}{w_i(t)}\right]$$

To compute population bioenergetics, one must calculate the gross biomass added to the population by the process of individual fish growth, referred to as gross growth, as follows:

$GG_{ij}(t)$ = gross growth of age-group i in area j during $[t, t+1]$

$$= GG1_{ij}(t) + GG2_{ij}(t)$$

where

$GG1_{ij}(t)$ = total biomass added to age-group i in area j by fish which survive $[t, t+1]$

$$= N_{i+1,j}(t+1)\left[w_{i+1}(t+1) - w_i(t)\right]$$

$GG2_{ij}(t)$ = total biomass added to age-group i in area j by fish which die during $[t, t+1]$

$$= \int_t^{t+1} [F_{ij}(t) + M_i]\, N_{ij}(x)\, w_i(t) \times [e^{g_i(t)(x-t)} - 1]\, dx.$$

Recruitment is assumed to occur in a knife edge fashion at the beginning of age 2, as:

$R_j(t)$ = number of fish recruited into age-class 2 at time t

$$= N_{2j}(t).$$

Growth

Growth parameters were calculated from length-at-age and weight−length data taken by U.S. observers aboard Soviet and Polish commercial fishing vessels during the 1976−80 fishing seasons (May−October). French et al. (1981) describe the sampling procedures. Briefly, random samples of trawl hauls were measured for length, and subsamples, stratified by length and sex, were taken for otoliths and round weight.

TABLE 1. Number of fish aged and lengths measured for analysis of growth data base.

		Eureka		Columbia	
Year	Stanza	No. otoliths read and fish weighed	No. lengths	No. otoliths read and fish weighed	No. lengths
1976	1	—	—	192	1055
	2	270	2102	1190	19050
	3	—	—	236	4465
1977	1	284	10811	1785	22235
	2	1335	46247	2469	42671
	3	—	—	1789	20590
1978	1	874	19241	1176	12593
	2	576	17007	2227	49008
	3	—	—	980	26872
1979	1	883	24790	189	12933
	2	411	31896	1142	51762
	3	—	—	501	51804
1980	1	—	—	446	14531
	2	231	12851	827	25394
	3	—	—	—	—

Dark (1975) described the determination of age from otolith. The following analyses are based on estimates (George Hirschhorn, Northwest and Alaska Fisheries Center, Seattle, WA 98112, personal communication, 1981) of mean lengths and weights at age stratified by:

1) Bimonthly *stanzas* — Stanza 1 = May, June; Stanza 2 = July, August; Stanza 3 = September, October,

2) Year — 1976–80,

3) Sex — Male, Female,

4) INPFC Statistical Area — Columbia, Eureka, Monterey (See Fig. 1).

The estimates are to be used in a model which attempts to represent the trophic dynamics of hake on an interannual and regional basis. Since the distances that hake migrate seem to be determined by size (length), and trophic demands determined by growth in weight, an attempt was made to examine the fundamental characteristics of both growth in length and growth in weight.

The following results summarize the problems associated with analysis of this hake growth data.

1) Both between and within age-classes, there is a latitudinal gradient in size, larger fish being found farther north than smaller fish. Dark (1975) also reported this tendency.

2) An apparent decrease in average length for ages 3–12 between stanza 1 (May, June) and stanza 2 (July, August) is a result of the larger fish of a given age group migrating into and through a given fishing area before the smaller fish. Therefore, for a given area, fish measured in stanza 2 are not necessarily the same fish that are measured in stanza 1.

These results reveal the problems inherent in estimating the true rate of growth in length from animals taken in a fishery where significant migration is present. Unfortunately, direct measurement of individual animal growth employing such methods as tagging is virtually impossible in this case. One hope, however, is that the quantification of annual growth increments on either otoliths or scales might reveal more about the dynamics of growth of hake than the present use of otoliths (George Hirschhorn, Northwest and Alaska Fisheries Center, Seattle, WA 98112, personal communication, 1981).

Table 1 shows the sample sizes for the stratified data base used in this analysis. The numbers of males and females examined were approximately equal.

Because Dark (1975) demonstrated that annual growth in length can be adequately described by the von Bertalanffy equation, I have focused on within season (May–October) growth, attempting to unravel biases inherent in the data. Instantaneous growth rates were calculated by taking the natural logarithm of the ratio of lengths in successive stanzas. Calculations were made by cohort, area, and sex. All rates were normalized to a *quarterly* (3 mo) time unit for comparative purposes. Thus, if for a given area and sex,

l_{ik} = average length of an individual of annual age i in time interval k,

then

g_{ik} = average instantaneous growth

$$= \begin{cases} \frac{3}{8} \ln\left[\frac{l_{i+1,1}}{l_{ik}}\right] & k = 3 \\ \frac{3}{2} \ln\left[\frac{l_{i,k+1}}{l_{i,k}}\right] & k = 1,2 \end{cases}$$

$$k = \text{time interval} = \begin{cases} 1 \text{ (June 1–August 1)} \\ 2 \text{ (August 1–October 1)} \\ 3 \text{ (October 1–June 1)} \end{cases}$$

The factor 3/8 normalizes an 8-mo growth rate to a 3-mo growth rate and the factor 3/2 normalizes a 2-mo growth rate to a 3-mo growth rate.

These estimates of instantaneous growth were then subjected to analysis of variance using the following linear model:

$$Y_{ijklm} = \mu + a_i + b_j + c_k + d_l + e_m + ac_{ik} + cd_{kl} + \epsilon_{ijklmn}$$

where

Y_{ijklm} = quarterly instantaneous growth rate for age i, area j, stanza k, sex l, year m,

$i = 2, \ldots, 12$

$j = 1$ {Columbia
2 {Eureka

$l = 1$ {Male
2 {Female

$m = 1976, \ldots, 1980$ — Year, and

$\epsilon_{ijklmn} \sim N(0, \sigma^2)$.

From the ANOVA, the only factors which were significant to

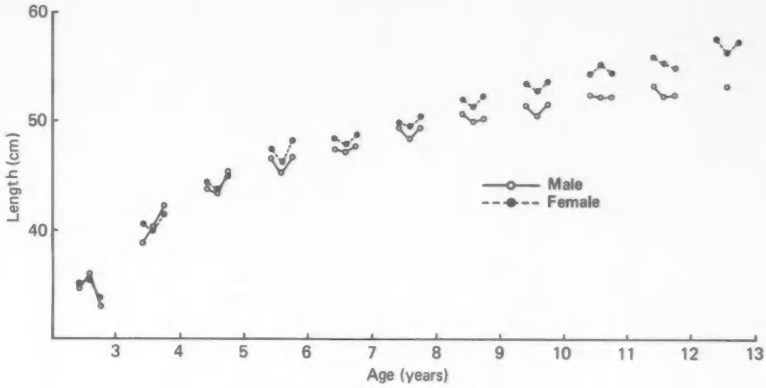

FIG. 2. Mean length of Pacific hake by age, sex, and time of year, 1976–80.

growth variability were Year ($P < 0.10$), Area ($P < 0.05$), and Stanza ($P < 0.01$). However, an important result was that, taking the estimates of the coefficients of the linear model, the expected values of quarterly instantaneous growth were:

$$E(g_k) = \begin{cases} -0.01332 & k = 1 \\ 0.02787 & k = 2 \\ 0.02349 & k = 3 \end{cases}$$

Thus, if one estimates instantaneous growth by area one obtains an estimated negative growth in length during time interval 1 (June 1–August 1), a result reflected in Fig. 2. This implies that, on the average, the fish which are harvested in an area in July–August are not among the fish that were harvested *in that area* in May–June.

To remove this apparent effect of migration on the estimates of instantaneous growth, I reestimated these rates under the following assumption: fish which are exploited in Eureka (May–June) are exploited in Columbia in (July–August). Thus,

$${}_mg_{i1} = \frac{3}{2} \ln \left[\frac{l_{i2}\,(\text{Columbia})}{l_{il}\,(\text{Eureka})} \right].$$

Since there were no estimates of average length (l_{ik}) for Eureka in Stanza 3,

$${}_mg_{i3} = \frac{3}{8} \ln \left[\frac{l_{i+1,1}\,(\text{Columbia})}{l_{i3}\,(\text{Columbia})} \right].$$

A similar ANOVA was done on these *modified* growth rates with Area no longer a factor and 1980 not included in Year (no suitable data). The only significant factor was Year ($P < 0.01$).

The following table gives the annual mean estimates of quarterly instantaneous growth and the June–August mean upwelling index at 45°N latitude (Andrew Bakun, Southwest Fisheries Center, Monterey, CA 93940, personal communication).

Year	$E({}_mg\,.\,.)$	June–August mean upwelling at 45°N
1976	0.04440	32
1977	0.00179	62
1978	0.01792	46
1979	0.00881	49

Although very little can be drawn from four data points, it appears that annual hake growth could be inversely related to the magnitude of upwelling in the feeding area off the northwest coast.

Figure 3 is taken from the same raw data that generated the modified growth rates above. Based upon this plot, I decided to look for ages where there might be differences in growth between stanzas by: (1) removing ages 2 and 12 due to a lack of data and (2) partitioning the analysis into two parts — one on ages 3–7 (ages where hake become mature and where sexual dimorphism should occur) and another on ages 8–11. ANOVAs on these two subsets reveal both Year ($P < 0.01$) and Stanza ($P < 0.10$) to be significant for ages 3–7 and Year ($P < 0.05$) only to be significant for ages 8–11. Furthermore individual orthogonal contrasts between time intervals reveal that for ages 3–7, differences in growth occur between what I will call spawning time (October 1–June 1) and feeding time (June 1–October 1). The expected values of instantaneous quarterly growth for ages 3–7 are

$$E({}_mg_{ik}) = \begin{Bmatrix} 0.02666 & k = 1, 2 \\ 0.01152 & k = 3 \end{Bmatrix} \quad i = 3, \ldots, 7,$$

and for ages 8–11 is

$$E({}_mg_{i\cdot}) = 0.00278 \quad i = 8, \ldots, 11.$$

The implications of this analysis in terms of estimates of model parameters are that:

1) Between ages 3 and 7, growth is seasonal. Using the estimates of instantaneous growth coefficients given above as indicators of relative growth during different parts of the year,

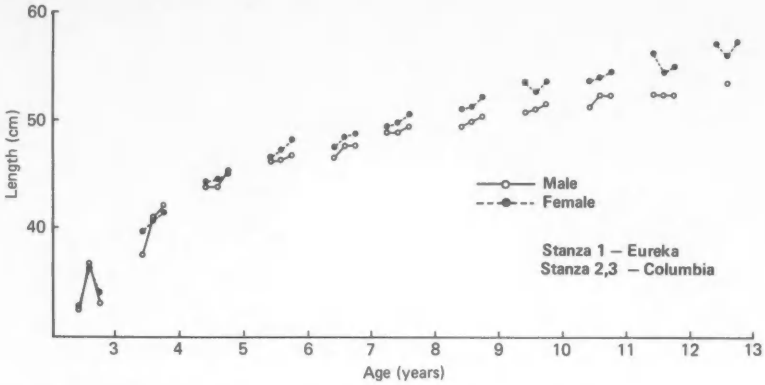

FIG. 3. Mean length of Pacific hake in Eureka (Stanza 1) and Columbia (Stanzas 2 and 3) by age-group and sex, 1975–79.

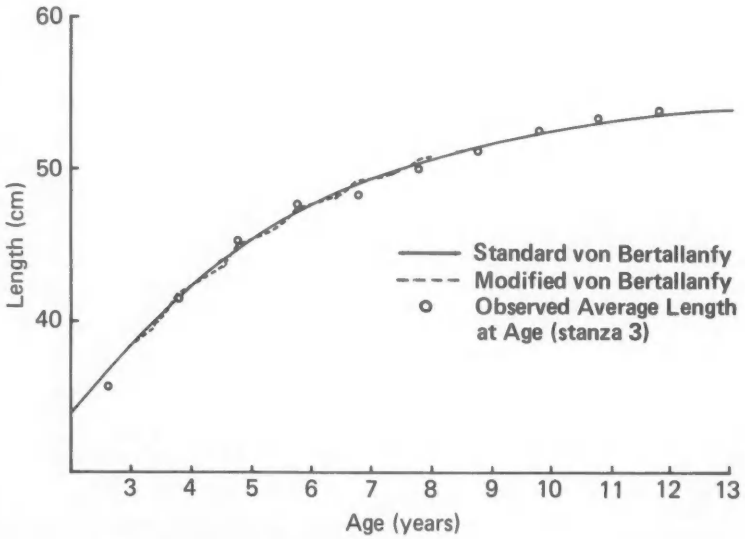

FIG. 4. Estimated length-age (sexes combined) of Pacific hake.

then

f_q = fraction of annual growth in length occurring during quarter q.

$$= \begin{cases} 0.17391 & \text{Quarter 1} \quad (\text{Jan.}-\text{Mar.}) \\ 0.25000 & \text{Quarter 2} \quad (\text{Apr.}-\text{June}) \\ 0.40218 & \text{Quarter 3} \quad (\text{July}-\text{Sept.}) \\ 0.17391 & \text{Quarter 4} \quad (\text{Oct.}-\text{Dec.}) \end{cases}$$

2) Fish older than 7 are growing so slowly that any seasonal differences are slight.

One aspect of this analysis that was rather disappointing was the inability to detect any significant differences in instantaneous growth between sexes. Sex–Age and Sex–Stanza interactions were examined in the ANOVAs but never were significant. Because the differences in size between sexes appears around ages 4–6 (Fig. 3), the apparent time of full maturity (Nelson and Larkins 1970), a more careful examination of the growth in length data around the ages of 4–5 might lead to insight into the mechanisms involved in the dimorphism.

To get annual increments of growth in length, the von Bertalanffy equation was fitted to the mean values of length

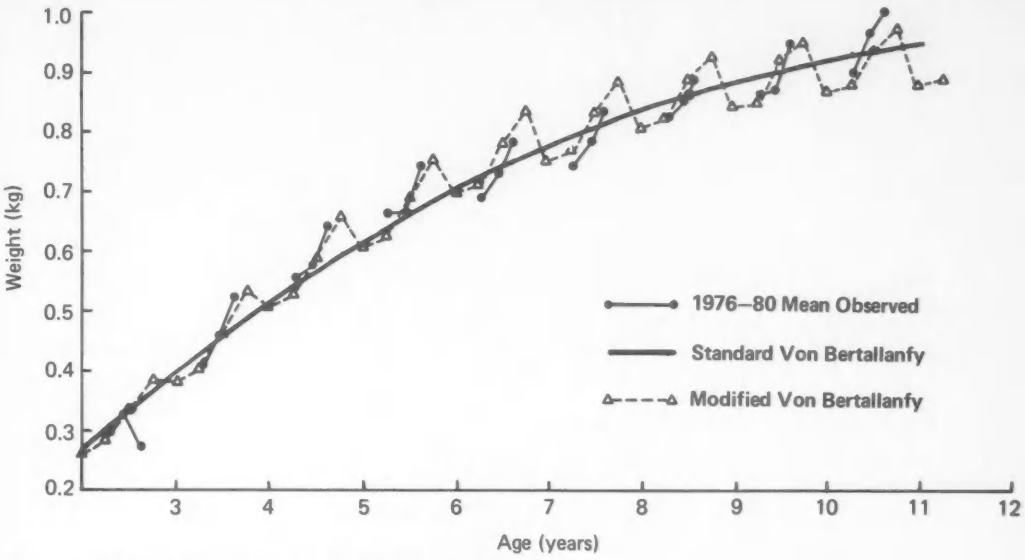

FIG. 5. Observed, standard, and modified weight-age for Pacific hake.

during September–October for ages 3 through 10 for 1976–79, averaged over sex and area, using a Fabens fit (Fabens 1965). The resultant equation and parameters are

$$l_t = \text{length in cm at annual age } t$$

$$= 55.402849\,[1 - e^{-0.260831\,(t-1.605444)}].$$

Partitioning the estimated annual instantaneous growth rates from the von Bertalanffy fit for ages 3–7 into quarterly values according to the estimates of f_q given above, a modified von Bertalanffy fit is obtained. Estimates of quarterly length at age for both of these fits are given in Fig. 4.

Weight-at-age has been traditionally obtained from length-at-age by employing the weight–length equation

$$w = a\,l^b.$$

Figure 5 (among other things) is a plot of mean weight at age (2–12) by Stanza and Sex for the 1975–80 U.S. observer data. Figure 6 gives mean weight against mean length by Age and Stanza. Sexes are combined in both figures to save space. These two figures reveal a significant amount of variability in weight within a given growing season which cannot be explained by a simple weight–length equation. An analysis of covariance was applied in an attempt to account for some of this variability. The model was a linear version of the weight–length equation,

$$Y_{ijklm} = \mu + a_i + b_j + c_k + d_l + e_m + b_{ik} X_{ijklm} + \epsilon_{ijklm}$$

$$= \text{natural logarithm of average weight of age } i,$$
$$\text{area } j, \text{ stanza } k, \text{ sex } l, \text{ year } m$$

$$X_{ijklm} = \text{natural logarithm of average length}$$

$$i = 2, \ldots, 11$$

$$j = \begin{cases} 1 \text{ Columbia} \\ 2 \text{ Eureka} \\ 3 \text{ Monterey} \end{cases}$$

$$k = \begin{cases} 1 \text{ (May–June)} \\ 2 \text{ (July–August)} \\ 3 \text{ (September–October)} \end{cases}$$

$$l = \begin{cases} 1 \text{ Male} \\ 2 \text{ Female} \end{cases}$$

$$m = 1975, \ldots, 1980.$$

The model was first tested for differences in slopes (b_{ik}) and none were significant. An analysis of covariance (intercepts) was then performed under the assumption that there is one common slope (see the following table).

Source	df	F
Year	5	67.39***
Area	2	5.40***
Sex	1	0.18
Age	9	21.31***
Stanza	2	92.42***
Covariate	1	3964.25***
Error	392	

***$P < 0.01$.

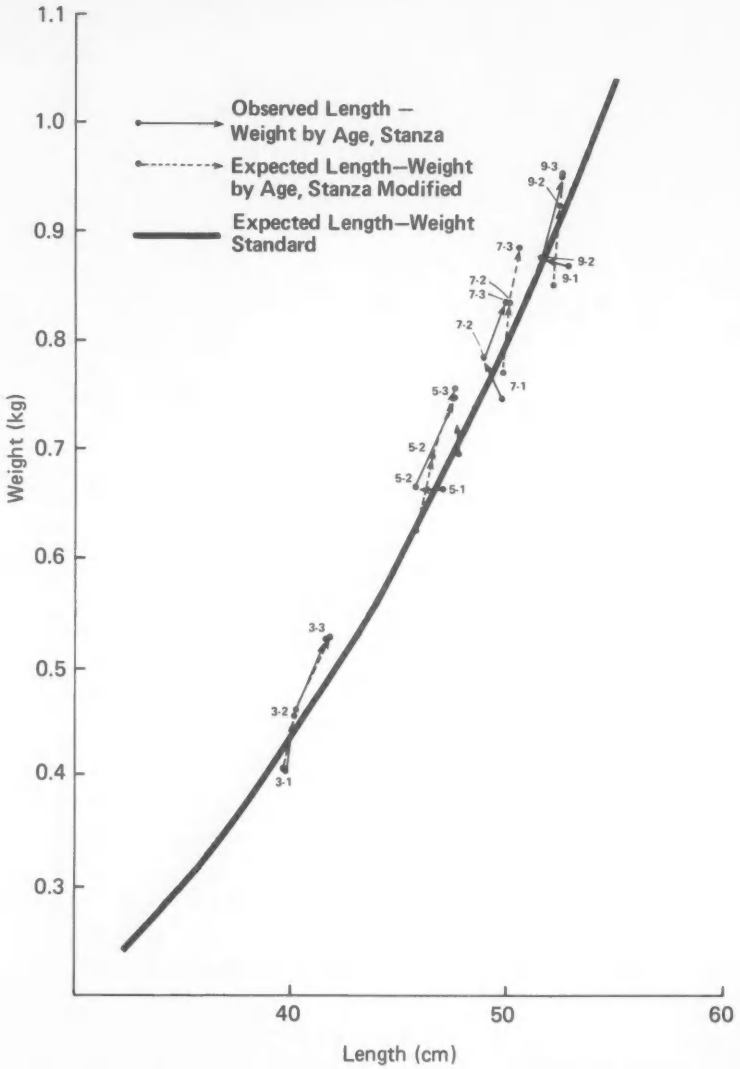

FIG. 6. Observed, standard, and modified length–weight of Pacific hake by age-group (sexes combined).

From the analysis both Age and Stanza are highly significant, which implies that an accurate representation of the within-season dynamics of weight necessitates use of the following weight–length equation (*Modified*) for sexes combined.

$$w_{ik} = a_{ik}\, l^{3.21976}$$

where the values of a_{ik} are given in Table 2. A single weight–length equation (*Standard*) was also fitted to the data and had the form

$$w = 0.001815\, l^{2.73343}.$$

Figure 6 also shows plots of the standard and modified weight–length relationships. Notice how all of the observations in Stanza 3 and all but one in Stanza 2 fall above

TABLE 2. Parameters for modified equation on the weight–length of Pacific hake.

$$w_{ik} = a_{ik}\, l^{3.21976}$$
$$i = 2, \ldots, 12; \quad k = 1, 2, 3$$
$$a_{ik}$$

Age	Stanza 1	Stanza 2	Stanza 3
2	0.000301	0.000320	0.000327
3	0.000294	0.000312	0.000319
4	0.000288	0.000306	0.000314
5	0.000280	0.000298	0.000305
6	0.000275	0.000292	0.000299
7	0.000265	0.000282	0.000289
8	0.000260	0.000277	0.000283
9	0.000254	0.000270	0.000276
10	0.000249	0.000264	0.000271
11	0.000243	0.000258	0.000264
12	0.000238	0.000252	0.000259

the standard line and all but one in Stanza 1 fall below the standard line. Finally, Fig. 5 also shows the standard and modified quarterly weight–age relationships used in the simulation model. The representation of within-season growth in weight is noticeably different between the two curves. Later I will examine the impact of these two representations of hake growth on the estimated trophic demands of the stock.

In summary, I would say that the major shortcomings of this analysis of hake growth are associated with the highly migratory nature of the population relative to the fishery, particularly in the first few months of the season, and the obvious lack of fit of annual growth in length to the von Bertalanffy equation. In addition the representation of the within season growth dynamics reflects only information gathered between May and October in the fishery. My guess is that its real amplitude is greater than represented in this work.

Mortality

Two sets of natural mortality rates are used in the simulation. The first assumes that the annual instantaneous natural mortality rate $M_i = 0.45$; $i = 2, \ldots, 12$. This is the average value of M presented in the Pacific Fishery Management Council (PFMC) Pacific Coast Groundfish Plan (Pacific Fishery Management Council 1981). The second uses the assumptions of Granfeldt (1979), Cushing (1973), and Laevastu and Larkins (1981):

a) Between hatching and the critical age (age at which most of the stock is fully mature), natural mortality is a density dependent function of age (size).

b) After the critical age, natural mortality shows a rather steady increase with age (approximately 10% per yr — Laevastu and Larkins (1981)) for 4–5 yr due to an increase of spawning stress, after which it undergoes irregular fluctuations.

Average age-specific natural mortality was thus estimated assuming that the critical age was age 5. This certainly seems reasonable from the literature (Bailey et al. 1982). The average increase rate in post-critical age natural mortality was

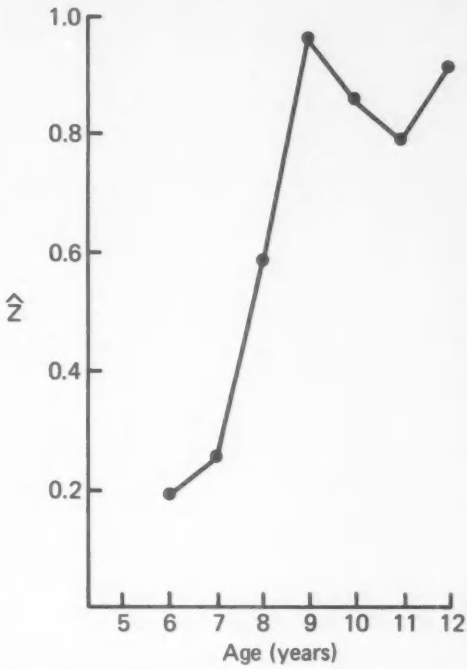

FIG. 7. Annual instantaneous total mortality for Pacific hake.

estimated from the 1973–80 mean age-structure of the commercial catch. Estimates of Z_i; $i = 6, \ldots, 12$, the average total annual instantaneous mortality rate, are given in Fig. 7. If one is willing to assume that on the average age-specific fishing mortality is constant from age 6 on, then one can fit the regression.

$$Z_t = F + M_o + M\,(t - 6); \quad t = 6, \ldots, 12$$

where

F = constant annual instantaneous fishing mortality rate.

M_o = baseline annual instantaneous natural mortality at age 6.

ΔM = average annual increase in natural mortality.

Using the above data, $(F + M_o) = 0.127$ and $\Delta\hat{M} = 0.146$. The following two factors lead one to believe that this estimate of ΔM might be an overestimate.

1) Preliminary cohort analyses indicate that on the average fishing mortality increases with age past age 6, and

2) Survey results (Dark et al. 1980; Beamish 1981) indicate that there is a tendency for larger, older fish to move into Canadian waters where they are unavailable to the U.S. fishery.

TABLE 3. Input data for Pacific hake for cohort analyses.

	Year	Age 3	4	5	6	7	8	9	10	11	Effort (10^3 days)
a) Option 1 — Standard weight–age Constant natural mortality											
Catch	73	54.94	9.51	21.34	39.52	24.72	22.61	21.13	10.14	4.44	6.31
in	74	0.94	162.41	22.24	38.49	48.02	27.89	12.36	3.88	1.77	8.68
numbers	75	2.71	3.72	129.12	21.98	23.67	38.22	17.25	7.44	3.72	11.52
in	76	37.37	29.70	30.03	188.20	28.03	14.02	5.01	1.00	0.33	9.21
millions	77	3.84	54.87	11.34	20.12	68.59	11.16	5.85	2.74	1.46	4.24
	78	4.28	8.15	49.57	9.39	19.88	37.28	5.39	2.35	1.11	2.99
	79	11.23	17.93	10.14	54.71	19.20	34.06	20.83	3.26	1.81	5.27
	80	18.36	10.75	10.39	11.48	25.01	11.72	18.00	9.18	2.66	3.20
M		0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	
b) Option 4 — Modified weight–age Laevastu–Cushing natural mortality											
Catch	73	52.66	9.11	20.46	37.87	23.70	21.67	20.25	9.72	4.25	6.31
in	74	1.00	153.94	21.09	36.48	45.51	26.44	11.71	3.68	1.67	8.68
numbers	75	2.58	3.54	123.03	20.93	22.54	36.39	16.43	7.09	3.54	11.52
in	76	32.25	28.01	28.32	177.49	26.43	13.22	4.72	0.94	0.32	9.21
millions	77	3.65	52.11	10.77	19.11	65.14	10.60	5.56	2.61	1.39	4.24
	78	4.07	7.74	47.08	8.92	18.88	35.41	5.11	2.23	1.05	2.99
	79	10.70	17.09	9.67	52.12	18.30	32.45	19.85	3.11	1.73	5.27
	80	17.65	10.33	9.99	11.03	24.03	11.26	17.30	8.82	2.55	3.20
M		0.278	0.210	0.195	0.257	0.357	0.457	0.557	0.657	0.757	

Both of these factors would tend to bias the estimate of ΔM upwards. Annual age-specific M was therefore estimated assuming (a) and (b) above, that the annual increase factor in postcritical M was 0.1 (Laevastu and Larkins 1981) and that

$$\sum_{i=2}^{12} \hat{M}_i = 11 \times 0.45 = 4.95.$$

Thus the total natural mortality of the simulated (ages 2–12) population is the same under both options. These estimates of M_i are in Table 3 under Option 4.

The annual growth and decay of an average unexploited hake cohort may be estimated using the four combinations of the two options for growth and mortality described above. Figure 8 is a plot of these curves and clearly shows that any differences in estimates of production due to growth would have to be due to the representation of seasonal effects in the modified weight–age option rather than any significant differences in fit to the von Bertalanffy equation between the two growth options.

A cohort analysis using the analytic formulation of Pope (1972) and Tomlinson (1970) was performed on the estimates of annual hake catch by age for 1973–80 to estimate age-specific fishing mortality rates and catchability coefficients. Separate cohort analyses were carried out for growth–mortality options 1 and 4 (See Fig. 8). The basic input data for the analyses are given in Table 3. The data limited the estimable ages to 3–11. The catch–effort data correspond to those reported in Bailey et al. (1982). Analyses were made using the backward solution (Tomlinson 1970) for each cohort assuming that each year ages 10 and 11 were exploited at the same rate. Pope (1972) shows that for a given cohort the error in the estimate of fishing mortality F_i for some age i (and subsequently catchability q_i) is proportional to the expression

$$\rho(F_i) = \left(\frac{1 - e^{F_i}}{F_i}\right) e^{-\sum_{k=i}^{t-1} F_k}$$

where

F_k = estimates of fishing mortality for that cohort at ages $k = i, \ldots, t-1$.

Letting

W_{ij} = weighting factor for age i in year j

$= 1/\rho^2(F_{ij})$,

the cohort analysis was performed by setting initial catchability coefficients

$q_{i,\,1980}$; $i = 3, \ldots, 10$ such that if

$$\bar{q}_{i\cdot} = \sum_{j=1973}^{1980} W_{ij}\,\hat{q}_{ij},$$

$$\text{Var}(\bar{q}_{i\cdot}) = \frac{\sum_{j=1973}^{1980} W_{ij}(\hat{q}_{ij} - \bar{q}_{i\cdot})^2}{7\sum_{j=1973}^{1980} W_{ij}}$$

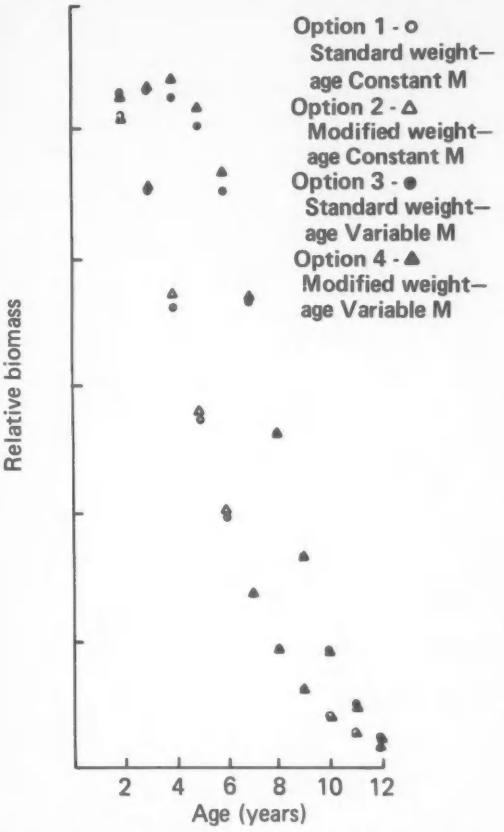

FIG. 8. Annual growth and decay of a Pacific hake cohort under various growth and mortality options.

$$\overline{CW}_{i\cdot} = \frac{1}{8}\sum_{j=1973}^{1980} CW_{ij}, \text{ and}$$

CW_{ij} = catch in weight of age i in year j,

then

$$\overline{CV} = \sum_{i=3}^{11} \overline{CW}_{i\cdot} \frac{\sqrt{\text{Var}\,(\bar{q}_{i\cdot})}}{\bar{q}_{i\cdot}}$$

is minimized. Since the primary objective of the analysis is to estimate age-specific catchability coefficients for the simulation, the cohort analysis was performed to minimize the average coefficients of variations of these age-specific catchability coefficients. The weighting factors (W_{ij}) were chosen to give greater weight to the more precise estimates of q_{ij}. The results of the analyses are given in Table 4. The estimates of mean stock biomass for Option 1 are about two times what they are for Option 4. The estimates of total hake biomass

TABLE 4. Summarized results of Pacific hake cohort analyses.

Year	Recruitment (millions) at age 3	Mean stock biomass (million t)	Age i	$\bar{q}_{i\cdot}$
a) Option 1 — Standard weight–age Constant natural mortality				
1973	4 100	2.302	3	0.00197
1974	2 126	2.474	4	0.00620
1975	1 248	2.190	5	0.00829
1976	3 916	2.916	6	0.01993
1977	936	2.386	7	0.03044
1978	1 295	2.131	8	0.04897
1979	1 115	1.858	9	0.05329
1980	3 575	2.593	10	0.04835
Mean	2 289	2.356		
CV	0.593	0.135		
b) Option 4 — Modified weight–age Laevastu–Cushing natural mortality				
1973	1 736	1.125	3	0.00450
1974	673	1.265	4	0.01185
1975	388	1.210	5	0.01416
1976	1 255	1.454	6	0.03072
1977	300	1.275	7	0.04290
1978	434	1.182	8	0.07121
1979	410	1.062	9	0.07711
1980	1 582	1.450	10	0.06982
Mean	847	1.253		
CV	0.691	0.113		

TABLE 5. Correlation of recruitment estimates from cohort analysis with Bailey's Year–Class Index.

Year–Class	Year–Class Index	R_3 (million individuals) Option 1	R_3 (million individuals) Option 4
1970	71.3	4 100	1 736
1971	11.7	2 126	673
1972	13.6	1 248	388
1973	117.7	3 916	1 255
1974	19.5	936	300
1975	14.2	1 295	434
1976	14.1	1 115	410
1977	38.9	3 575	1 582
<		0.804	0.691

from the NWAFC trawl-hydroacoustic surveys of July–September 1977 and 1980 are 1.199 million t (Dark et al. 1980) and 1.519 million t (Marty Nelson and Thomas Dark, Northwest and Alaska Fisheries Center, Seattle, WA 98112, personal communication), respectively. Certainly the survey estimates tend to correspond to the cohort analysis estimates of mean stock biomass much better when Option 4 is employed than when Option 1 is employed. It is apparent that if age-specific catchability has been relatively constant between 1973 and 1980 the cohort analysis indicates that stock biomass has remained relatively constant over that time interval. Finally the estimates of recruitment at age 3 (R_3) provided by the cohort analyses may be correlated with Bailey's corresponding year-class index (YCI) (Kevin Bailey, University of

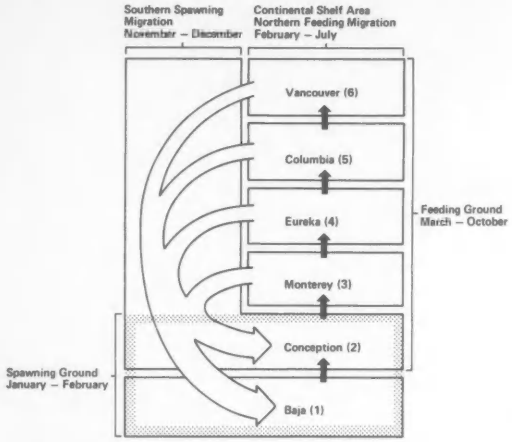

FIG. 9. The annual migration cycle of Pacific hake.

Washington, Seattle, WA 98195, personal communication) (Table 5). The linear correlations are $r = 0.804$ for Option 1 and $r = 0.691$ for Option 4.

Thus, the basic question posed in this section is whether or not natural mortality is a variable function of age. The results obtained from cohort analysis are markedly different, especially in terms of estimates of stock biomass, between estimates made under the assumption of constant natural mortality and those made under the assumption of variable natural mortality. It seems that, perhaps, one must use more than goodness of fit as a criterion for evaluating the validity of various representations of mortality. My overriding assumption is that the 1977 (Dark et al. 1980) and 1980 NWAFC groundfish surveys give reasonably accurate estimates of exploitable hake biomass.

Migration

The annual migration cycle of Pacific hake is described by Alverson and Larkins (1969) and Bailey et al. (1982). Figure 9 gives a schematic representation of the hake migration as it is represented in the simulation model. The simulated spawning migration takes place over a 2-mo period (November, December) and the simulated feeding migration over a 6-mo period (February–July). It is assumed that animals migrating north migrate through the inshore fishing grounds over the continental shelf. The average distance an animal of a given age migrates is a function of its average size with the larger animals tending to migrate farther to the north.

For a given age i, the instantaneous migration rate is calculated after a model of Bledsoe (L. J. Bledsoe, University of Washington, Seattle, WA 98195, personal communication) for North Pacific albacore (reported in Kume and Bartoo 1981) as follows.

$I_i^{j-1,j}(t)$ = instantaneous migration rate of age-group i from area $j-1$ to area j at time t

$$= \frac{a_i^j}{b_i^j \sqrt{2\pi}} e^{-\frac{1}{2}\frac{(t-t_{oi}^j)}{(b_i^j-1)^2}}$$

a_i^j = total instantaneous migration of age i from area $j-1$ to area j (1/d)

t_{oi}^j = time of maximum migration from area $j-1$ into area j (day of year)

b_i^j = standard deviation of t

$$= \sqrt{\sum_{k=2}^{j-1} \frac{(MR_i^k)^2}{4}}$$

MR_i^k = mean residence of age i in area k (days).

Thus the northern feeding migration between two adjacent areas $j-1$ and j is normally distributed with a specified time of peak migration and a variance based on the mean residence times in those and previously occupied areas. The parameters of the model were estimated from results of the July–September 1977 NWAFC groundfish survey (Dark et al. 1980). The relative hake distribution over area by age for the survey is given in Table 6. From these, and the estimated distances between areas (m_j), the mean distance traveled for each age (d_i) can be calculated. Then, assuming that on the average it takes an animal 120 d (4 mo) to travel that distance, the mean swimming speed (s_i) was calculated. These are also given in Table 6. Parameters for the model were then calculated (Table 7) assuming that the areal distributions reflected by the survey are indicative of stable distributions on the feeding grounds after the feeding migration is complete.

Plots of the relative areal distribution of ages 3 and 7 hake (unexploited) as a function of time of the year are given in Fig. 10. The spawning migration for all ages is assumed to start at the beginning of November and last through December. Little is known about the relative distribution of the spawning population between the southern California (Conception) and Baja California (Baja) spawning grounds. To accommodate the hypothesis of Smith,[1] that large adults spawn farther south, the age-specific distribution of hake on the Baja ground was assumed to be the same (mirror image) as the distribution of those same adults on the Vancouver feeding ground.

The main problem with this analysis of hake migration is that it is based on information generated in one resource survey. To use the migration parameter estimates one must make the assumption that the stock distribution, both in terms of age and relative biomass, over the feeding ground is relatively constant from year to year, even as the total stock biomass varies. Preliminary results for the 1980 NWAFC groundfish survey (Martin Nelson and Thomas Dark, Northwest and Alaska Fisheries Center, Seattle, WA 98112, personal communication) tend to bear this out. Still, with only

[1]Smith, P. Pacific hake larval distribution and abundance, 1951–1975. Southwest Fish. Cent. Admin. Rep. LJ-75-83. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 6. The 1977 groundfish survey data used to estimate migration parameters of Pacific hake.

Age	Vancouver	Columbia	Eureka	Monterey	Conception	$\bar{d}_i$	$\bar{s}_i$
2	0.000	0.003	0.216	0.768	0.012	660	5.499
3	0.000	0.049	0.431	0.477	0.042	791	6.594
4	0.141	0.153	0.446	0.257	0.003	1084	9.035
5	0.273	0.227	0.433	0.066	0.001	1303	10.856
6	0.276	0.331	0.320	0.072	0.000	1344	11.197
7	0.366	0.297	0.275	0.062	0.000	1401	11.675
8	0.306	0.408	0.232	0.052	0.001	1403	11.690
9	0.365	0.379	0.213	0.042	0.001	1440	12.000
10	0.189	0.483	0.256	0.071	0.002	1340	11.166
11	0.282	0.380	0.224	0.112	0.003	1345	11.212
12	0.021	0.767	0.087	0.125	0.001	1303	10.856
m_j	1774	1440	1051	562	0		

m_j = estimated distance from spawning ground to center of area j (km)
$\bar{d}_i$ = mean distance traveled for age i (km)
$\bar{s}$ = mean swimming speed (km/d)

two points in time, one runs out of degrees of freedom and starts using degrees of imagination rather rapidly.

Model Calibration and Validation

Francis (1977) describes the process of model validation as a subjective pursuit which, more than anything else, helps display the modeler's intuition concerning the most suitable analytic form or parameter values for attaining specific objectives. In the case of HAKE, the primary calibration and validation criteria are the ability of the model to mimic the areal, time, and age distribution of the observed catch during 1977–80, the only years for which these statistics are available in any reliable detail. The calibration–validation run of the model was made for 1977–80 with:

1) Initial age-specific population numbers (1977) derived from the cohort analysis.

2) Recruitment numbers derived from the cohort analysis back calculated to the beginning of age 2.

3) Effort summarized in Table 8.

4) Estimates of average age-specific catchability from the cohort analysis adjusted as follows:

For a given year x let

$_xq_{ij'k}$ = catchability of age i in area j' during quarter k.

$j' = 1$ for the southern two fishing areas (Monterey, Eureka)

$j' = 2$ for the northern two fishing areas (Columbia, Vancouver),

$_x\hat{q}_i$ = estimated catchability from the cohort analysis;

$_xYN_{ij'}$ = yield in numbers,

$$_xYN_{i\cdot} = \sum_{j'} {}_xYN_{ij'},$$

$_xf_{j'}$ = effort in area j',

$$_xf_{\cdot} = \sum_{j'} {}_xf_{j'}, \text{ and}$$

$\rho_{ij'}$ = fraction of age i hake contained in area j' (from 1977 survey).

If

$$_xYN_{ij'} = {}_xq_{ij'\cdot}\, {}_xf_{j'}\, \rho_{ij'}\, {}_x\bar{N}_{i\cdot}$$

$$_xYN_{i\cdot} = {}_xq_{i\cdot\cdot}\, {}_xf_{\cdot}\, {}_x\bar{N}_{i\cdot}$$

then

$$_xq_{ij'\cdot} = \frac{{}_xYN_{ij'}\, {}_xq_{i\cdot\cdot}\, {}_xf_{\cdot}}{{}_xYN_{i\cdot}\, \rho_{ij'}\, {}_xf_{j'}},$$

and

$$_{\cdot}\bar{q}_{ij'\cdot} = \sum_x {}_x\hat{q}_{ij'\cdot}$$

This gives an estimate of average age-specific catchability for the southern and northern two fishing areas.

The model was then run for 1977 and 1978 and calibrated by employing time-specific availability factors for each of the two areas in such a manner that

$$q_{ij'k} = {}_{\cdot}q_{ij'\cdot}\, a_{j'k}.$$

The values of $\{a_{j'k} : j' = 1, 2, k = Q2, Q3, Q4\}$ were adjusted (calibration) to give the best fit of the simulated to the observed catches and age-structures for 1977 and 1978. For validation purposes, the model was then allowed to run for 1979 and 1980 with the observed effort. The observed and simulated catches are given in Table 8. The final parameter values of catchability and availability are given in Table 9. The model was run in two modes — HAKE/M0D1 uses standard weight–age and constant natural mortality;

TABLE 7. Migration parameter estimates for Pacific hake.

Age		Conception $j = 2$	Monterey $j = 3$	Eureka $j = 4$	Columbia $j = 5$	Vancouver $j = 6$
2	MR_2^j	38	128	51	83	
	a_2^j		4.423	0.252	0.014	0.000
	b_2^j		9.50	33.38	35.73	41.32
	t_{o2}^j		79	162	252	319
3	MR_3^j	32	107	42	76	
	a_3^j		3.170	0.697	0.108	0.000
	b_3^j		8.00	27.92	29.83	35.37
	t_{o3}^j		76	146	220	279
4	MR_4^j	23	77	31	55	
	a_4^j		5.809	1.356	0.506	0.653
	b_4^j		5.85	20.30	21.71	25.75
	t_{o4}^j		72	122	176	219
5	MR_5^j	19	65	26	46	
	a_5^j		6.908	2.717	0.768	0.790
	b_5^j		4.87	16.89	18.06	21.42
	t_{o5}^j		70	112	157	193
6	MR_6^j	19	63	25	45	
	a_6^j		4.605	2.631	1.064	0.606
	b_6^j		4.72	16.37	17.51	20.77
	t_{o6}^j		69	110	154	189
7	MR_7^j	18	60	24	43	
	a_7^j		4.605	2.781	1.227	0.803
	b_7^j		4.50	15.66	16.77	19.92
	t_{o7}^j		69	108	150	183
8	MR_8^j	18	60	24	43	
	a_8^j		6.908	2.956	1.406	0.560
	b_8^j		4.52	15.69	16.77	19.89
	t_{o8}^j		69	108	150	183
9	MR_9^j	18	59	23	42	
	a_9^j		6.908	3.169	1.503	0.675
	b_9^j		4.40	15.28	16.34	19.38
	t_{o9}^j		69	107	148	180
10–12	MR_t^j	17	57	23	41	
	a_t^j		7.601	3.507	1.558	0.680
	b_t^j		4.27	14.84	15.87	18.82
	t_{ot}^j		69	106	145	177

HAKE/M0D2 uses modified weight–age and Laevastu–Cushing natural mortality. The relative fit, in terms of both the absolute magnitude and the relative age-structure of the catch, for the two modes is approximately the same. The trend of the availability factors (Table 9) over time of the year reflects the movement of the fishing fleet relative to the resource. The fishery generally begins in May, June, and July in southern Columbia and Eureka and then moves north into Columbia and Vancouver in August, September, and October until the fish start their spawning migration moving offshore and then south from the fishing grounds. The Soviet hydroacoustic survey of 1978 (Stepanenko 1979) certainly reflects this with an estimated order of magnitude increase in biomass of hake in Columbia between June–July and August–September.

Certainly the major shortcoming of this validation work on a model as complex as HAKE is the absence of a detailed sensitivity analysis of the effects of possible errors in parameter estimates on model output. In light of the obvious uncertainty about model parameter values, particularly those associated with mortality and migration, a sensitivity analysis along the lines proposed by Rose (1982) is in order. However, I leave that to another time and another investigator.

Bioenergetics

The design of HAKE makes it useful for examining the bioenergetics of the coastal stock of Pacific hake. The model incorporates sufficient resolution to reflect the interaction between age structure and migration, important factors in bioenergetic calculations.

For a given time interval, dt, and area, i, knowledge of the age-structure and growth of the hake occupying that area drives the calculation of biomass consumed by hake. Suppose we have a fish of average weight $\bar{w}$ (grams). Then, based on Jones and Johnston (1977) and Sharp and Francis (1976):

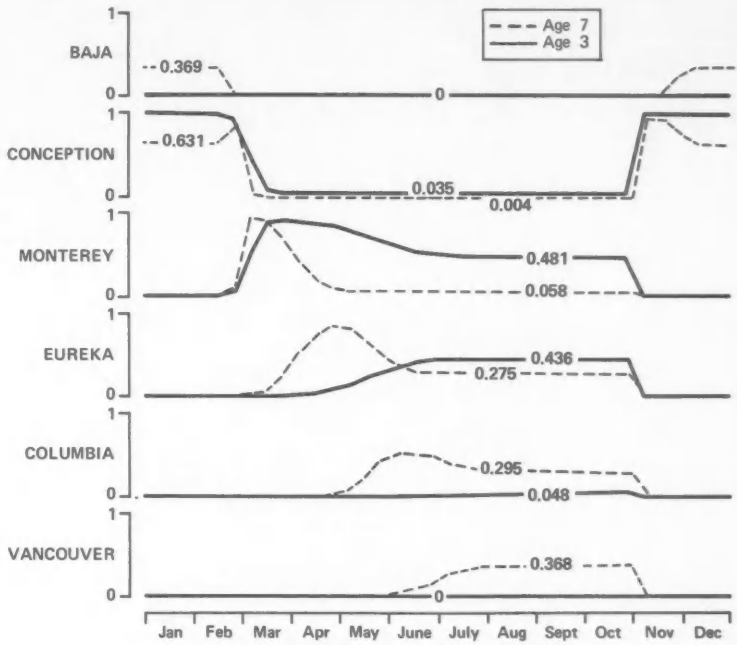

FIG. 10. Simulated relative areal distribution of ages 3 and 7 Pacific hake.

TABLE 8. Observed and simulated total catch (kt) and effort (1000 standard BMRT[a] days on ground).

Year			Vancouver	Columbia	Eureka	Monterey	Total
1977	Effort	Observed	0.168	2.927	1.146	—	4.241
	Catch	Observed	5.180	85.483	41.549	—	132.212
		Option 1	5.053	83.870	44.161	—	133.084
		Option 4	5.588	87.135	42.750	—	135.473
1978	Effort	Observed	0.182	2.166	0.610	0.031	2.989
	Catch	Observed	6.450	70.989	25.890	0.750	104.079
		Option 1	6.003	69.349	24.446	0.486	100.284
		Option 4	6.278	69.450	23.429	0.453	99.610
1979	Effort	Observed	0.402	3.583	1.273	0.006	5.264
	Catch	Observed	12.130	76.300	47.130	0.285	135.845
		Option 1	11.316	101.516	45.766	0.109	158.707
		Option 4	11.104	95.496	42.471	0.907	149.978
1980	Effort	Observed	0.346	1.989	0.863	—	3.198
	Catch	Observed	19.120	58.090	13.490	—	90.700
		Option 1	11.201	61.260	26.754	—	98.215
		Option 4	10.679	56.321	23.898	—	90.898

[a]BMRT = Soviet-type factory stern trawler.

FE = food energy intake (kcal/dt) (1 kcal = 4186.8 J) where

$= GE + ME$, and

GE = energy demands for growth and reproduction (kcal/dt)

$= GG/\epsilon$

GG = gross growth (g/dt)

ϵ = gross growth efficiency (g/kcal)

$= 0.79\ \bar{w}^{-0.15}$ (Jones and Johnston 1977),

TABLE 9. Estimates of catchability and availability of Pacific hake.

	q_{ij}			
	$j = 1$ Monterey, Eureka		$j = 2$ Columbia, Vancouver	
Age i	M0D1	M0D2	M0D1	M0D2
2	0.005	0.010	0.001	0.002
3	0.010	0.020	0.002	0.005
4	0.018	0.040	0.013	0.029
5	0.031	0.058	0.014	0.027
6	0.050	0.076	0.018	0.028
7	0.107	0.133	0.054	0.066
8	0.179	0.210	0.085	0.098
9	0.131	0.152	0.073	0.084
10	0.124	0.143	0.054	0.068
11	0.079	0.082	0.058	0.067
12	0.080	0.091	0.060	0.067

Availability (Raw)

		a_{jk}	
		$j = 1$	$j = 2$
	Quarter (k)	Monterey, Eureka	Columbia, Vancouver
M0D1	Q2	0.679	4.677
	Q3	1.332	2.164
	Q4	—	10.898
M0D2	Q2	0.700	4.770
	Q3	1.238	2.199
	Q4	—	11.449

ME = energy for maintenance

= (0.01904) DDT $\bar{w}^{0.8}$ (kcal/dt) (Jones and Johnston 1977), and

DDT = number of dt's per day.

Then, if 1 g wet food intake = 1 kcal (Sharp and Francis 1976),

FC = wet weight of food ingested (g/dt)

= FE.

Typical values for daily consumption of 2, 4, 6, and 8-yr old hake during the spring–summer (April–September) growth period, using M0D2 parameters are given below:

Age	$\bar{w}$ (g)	GG (g/d)	ϵ (g/kcal)	GE (kcal/d)	ME (kcal/d)	FC (g/d)	BWD (%)
2	336	0.553	0.33	1.676	3.675	3.675	1.094
4	594	0.734	0.30	2.423	3.153	5.575	0.939
6	778	0.663	0.29	2.278	3.912	6.190	0.796
8	880	0.559	0.29	1.956	4.318	6.274	0.713

Note that these estimates are only for the portion (April–September) of the year where significant feeding occurs.

The estimated percentage body weight consumed per day (BWD) by hake in this model is small compared with published values of other gadoids (Table 10). Remember that the above hake values are for their feeding-growing season whereas the values given below are annual. Annual values for hake would be in the range of 0.4–0.5% BWD.

TABLE 10. Estimated percentage body weight consumed per day (BWD) for various gadoids.

Source	Species	BWD(%)
Cohen et al. (1982)	Silver hake 1964–66	1.324
	1973–75	1.342
Cohen et al. (1979)	Cod 1964–66	0.777
	1973–75	0.904
Jones and Johnston (1977)	Whiting — $\bar{w}$ = 987	1.134
	$\bar{w}$ = 594	1.397
	$\bar{w}$ = 363	0.715
	$\bar{w}$ = 648	1.136

To make estimates of hake population bioenergetics, values of annual production (P), production to average biomass ratio ($P/\bar{B}$), consumption (C), and consumption to average biomass ratio ($C/\bar{B}$) were calculated from simulations of HAKE for 1973 through 1980 following the methods of Cohen et al. (1979). In this paper, production is defined as the gross addition of biomass due to growth (gross growth). Annual computations were made by INPFC area. Geometric mean annual $P/\bar{B}$, $C/\bar{B}$, and $R/\bar{B}$ (recruitment to biomass) ratios were calculated for the 8-yr period. Parallel runs of the model were made in exploited (E) and unexploited (U) modes. The exploited mode starts in January 1973 with the initial conditions estimated by the cohort analysis and imposes the observed 1973–80 fishing effort on the stock. The unexploited mode starts in January 1973 with the stock in unexploited equilibrium, based on average observed recruitment from the 1973–80 cohort analysis and runs an unexploited simulation inputting the appropriate estimated recruitment values derived from the cohort analysis. To compare bioenergetic estimates using the two different representations of growth (standard and modified weight–age), two separate sets of simulations were made. Variable age-specific natural mortality (Laevastu–Cushing) was used in all simulations since it seemed to provide the most realistic estimates of population biomass. The results of the analysis are summarized in Table 11.

The following points summarize the results:

1) Average biomass would have been 27% greater under virgin (unexploited) conditions than under the observed fishing patterns. Most of that increased biomass would have occurred in the northern areas.

2) Production due to growth would have been approximately the same in the exploited and unexploited situation; however, it is estimated to be, on the average, 9% greater under modified growth than under standard growth.

3) The distribution of production is weighted much more heavily toward the feeding and fishing areas (Monterey, Eureka, Columbia, and Vancouver) under modified growth than under standard growth. In fact, production in those feeding areas is estimated to be approximately twice under modified growth what it is under standard growth.

4) Consumption of hake would have been 17% greater under unexploited conditions than under the observed exploited condition and only 7% greater under modified growth

TABLE 11. Summarized results of Pacific hake bioenergetics simulations.

Mode	Growth		Total (Kt)	Mean percent composition				
				Baja–Conception	Monterey	Eureka	Columbia	Vancouver
Exploited	Standard	$\bar{B}$	1532	35	32	22	7	4
		$\bar{P}$	322	37	40	18	4	1
		$\bar{R}$	260	100	—	—	—	—
		$\bar{C}$	2206	36	36	20	5	3
	Modified	$\bar{B}$	1548	35	31	23	7	4
		$\bar{P}$	356	3	55	33	8	1
		$\bar{R}$	260	100	—	—	—	—
		$\bar{C}$	2337	19	42	28	8	3
Unexploited	Standard	$\bar{B}$	1945	35	27	22	10	6
		$\bar{P}$	331	36	38	18	5	3
		$\bar{R}$	260	100	—	—	—	—
		$\bar{C}$	2567	36	32	21	8	3
	Modified	$\bar{B}$	1964	34	27	23	10	6
		$\bar{P}$	353	−4	53	37	11	3
		$\bar{R}$	260	100	—	—	—	—
		$\bar{C}$	2749	18	37	29	11	5

than under standard growth.

5) As with production, the distribution of consumption is weighted more heavily toward the summer feeding areas under modified growth than under standard growth (roughly a 40% difference in Eureka, Columbia, and Vancouver).

I believe that the simulations of bioenergetics under the modified growth are a much more realistic representation than under standard growth. This is further indicated because hake do not feed extensively on the winter spawning grounds off the Conception and Baja California areas. Thus they must lose weight in winter and regain it during the spring–summer–fall feeding period. Under modified growth, the average (geometric mean of exploited and unexploited ratios) ratio of total production to biomass ($P + R/\bar{B}$) is 35% per year (around 600 thousand t total production under both exploited and unexploited conditions). The model therefore, estimates that moderate levels of fishing (an average annual 1973–80 catch of around 160 kt) has a negligible effect on gross production of the hake resource. Apparently, only about one-third of that production can be diverted into the fishery. I speculate on the relationship and implications of these estimates to those of Laevastu and Favorite (1977). They calculate an ecosystem internal consumption at minimum sustainable equilibrium levels for west coast roundfish, of which hake is the major component, at 82% per year. In an unexploited population of 2.0 million t, this would translate into an ecosystem internal consumption of post-recruit (ages 2+) of around 1.6 million t. Since I estimate total production of the unexploited 2+ stock to be only around 600 kt per year and the fishery is capable of taking, at most, around 200 kt on a sustained basis (Francis et al. 1982), this implies an ecosystem internal consumption of 2+ hake of no more than 400 kt, or about 20% of the average biomass, per year. The most likely reason for the discrepancy between these two approaches for estimating production is that Laevastu and Favorite (1977) are estimating ecosystem internal consumption of both adults and juveniles (50% of their roundfish biomass is in pre-fishing juveniles) and that the consumption of juveniles is much higher than that of adults, whereas I am estimating consumption of adults only. If ecosystem internal consumption of a particular species is approximately equal to that which it consumes, corrected for trophic efficiency, and

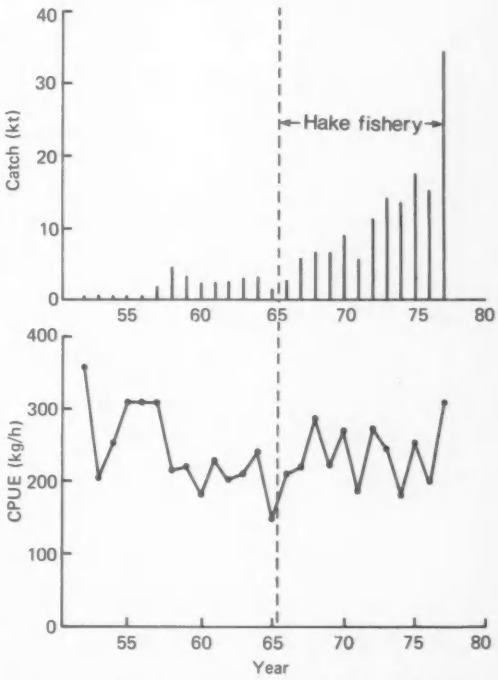

FIG. 11. Catch and catch-per-unit-effort (CPUE) of pink shrimp off Washington, Oregon, and California, 1952–77.

if an unexploited population of hake consumes 2749 kt, then the ecosystem internal consumption of that population should be between 275 and 550 kt per year, which seems to be "in the ballpark." In addition, under modified growth the average annual consumption to biomass ratio is 1.454 which translates to an average daily consumption of 0.398% BWD, considerably less than the estimates from the literature for similar species given in Table 10.

The following table compares the estimated hake consumption by area under unexploited (C_U) and exploited (C_E) conditions.

	BC-Conc.	Monterey	Eureka	Columbia	Vancouver	
$\bar{C}_U - \bar{C}_E$ (kt)	51	36	143	115	67	412

Thus, the estimated difference in total consumption by hake between unexploited and exploited conditions is around 412 thousand t per year. The most pronounced impact of this difference would be felt in the INPFC Eureka and Columbia areas. One can use these results to speculate on what impact this difference has on the pandalid shrimp fishery off the coasts of northern California, Oregon, and southern Washington, basically the Eureka and Columbia areas. Livingston (Patricia Livingston, Northwest and Alaska Fisheries Center, Seattle, WA 98112, personal communication) reports a range of from 0.3 to 4.4% as the fraction of pandalid shrimp in the diets of whiting collected off Oregon and Washington in 1977 and 1980. Extrapolating, this would imply that, between 1973 and 1980, the removal of whiting through fishing has on the average reduced the ecosystem internal consumption of pandalid shrimp in the Eureka and Columbia areas by 800 to 11 000 t. Assuming that no other predators pick up the slack, this shrimp would be available to the fishery. Figure 11 gives the trends of catch and CPUE for the pink shrimp (Pacific Fishery Management Council 1979) off the coast of Washington, Oregon, and California. The following table gives the average catches (kt) and catch per unit of effort (CPUE) (kg/h trawled) for pink shrimp during the pre- and post-hake fishery periods.

	1952–65	1966–77
Avg. catch (kt)	1.8	12.0
Avg. CPUE (kg/h)	274	269

Assuming that effort was standardized properly, these results indicate that the pink shrimp fishery could have replaced hake as a predator on shrimp, and that this could have happened with shrimp being a rather minor item in the hake diet. Obviously this extrapolation is made under the assumption of a rather simple community structure. However, one cannot ignore the implied linkages.

There is no doubt that this investigation of the bioenergetics of Pacific hake is highly speculative and probably raises more questions than it answers. However, that is precisely the point. If, in fact, the bioenergetics of hake are realistically represented, how might an awareness of them be an aid to making fisheries management decisions. My feeling is that the reason speculation about trophic dynamics of commercially important species has not been used to aid in fisheries management has to do with the extreme difficulty in validation of the trophic parameters. As a matter of fact, one wonders whether a deterministic representation of the feeding process makes any sense at all. If it does, then here is an attempt to study it, in considerable detail, for a single commercially important fish stock. In this case trophic demands are predominantly driven by the results of a careful representation of the growth process. The results are markedly different from previous published analyses on "similar" species. The question then becomes, how informative is this attempt to represent the trophic dynamics of a commercially important species? Does it provide insight which might be helpful in developing management policies oriented more heavily towards the total ecosystem?

Summary

This paper presents an attempt to explore both the population and trophic dynamics of the coastal stock of Pacific hake. An attempt was made to investigate and quantify certain facets of the basic population biology of the stock. An age-structured computer simulation model, entitled HAKE, was used as the central focus of this analysis. The results can be summarized as follows:

1) Both between and within age-classes, hake stratify by size on a latitudinal gradient, with the larger fish tending to move farther north than the smaller fish.

2) Two growth relationships of weight on age are derived for hake, one assuming that growth is uniform throughout the year and a second assuming that growth is seasonal (during the winter, November–March, spawning season adults between ages 4 and 11 lose a minimum of between 5 and 10% of their total body weight and during the April–October feeding season gain a minimum of between 11 and 30% of their initial body weight). These two relationships provide markedly different estimates of trophic demands. The distribution of both production and consumption is weighted more heavily toward the summer feeding areas (off northern California, Oregon, and Washington) under seasonal growth than under uniform growth.

3) Two representations of age-specific natural mortality (M) are explored. One assumes that M is constant as a function of age. The other assumes that between hatching and the critical age M is a density dependent function of age and, after the critical age, M increases with age for 4 to 5 yr, after which it undergoes irregular fluctuations. Comparisons of results of cohort analyses employing these two representations of M indicate that the latter is more realistic.

4) Results of simulations of adult (ages 2–12) stock bioenergetics indicate that

a) Whereas production due to growth does not seem to vary much as a function of exploitation, it is greater under the seasonal growth option than the uniform growth option.

b) The average ratio of total annual production (growth + recruitment) to average biomass is 0.35 (around 600 thousand t total annual production).

c) Average daily consumption is around 0.4% BWD which is considerably less than estimates from the literature for similar species.

d) The increased pink shrimp catch off the Washington–Oregon–California coast since the inception of the hake fishery in 1966 could be attributable to an increase in shrimp production as a result of decreased hake predation on shrimp.

Acknowledgments

Thanks are due to numerous scientists at the Northwest and Alaska and Southwest Fisheries Centers for freely sharing their ideas and making data available. Particular thanks go to Kevin Bailey and George Hirschhorn, without whose helpful insights much of the work reported in this paper would have been impossible to carry out. I thank M. Hisley, W. Silvert, and an anonymous reviewer for their careful review of this manuscript. I also thank Tom Dark, George Hirschhorn, and Taivo Laevastu for reviewing an earlier version of this manuscript.

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Age and Growth of the Shortfin Mako, *Isurus oxyrinchus*, Using Four Methods[1]

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PRATT, H. L., JR., AND J. G. CASEY. 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. 40: 1944–1957.

Age and growth rate of shortfin mako, *Isurus oxyrinchus*, captured by hook and line between 1961 and 1981 were determined using four methods: (1) temporal analysis of length–month information, (2) results of tagging data, (3) length–frequency analysis, and (4) ring counts on vertebrae. A temporal analysis of length–month information relating size to age for individuals less than 150 cm fork length (*FL*) was used to determine size (60–70 cm *FL*), time of birth (late spring), and early growth rate (50 cm/yr for ages 0–I, 32 cm/yr for ages I–II). This growth rate was used as a basis for interpreting the accuracy of other methods. Annual growth rates were calculated from 32 tag–recaptured mako sharks and resolved graphically into a growth curve. Length–frequency modes extended age estimates to intermediate-sized makos. Counts of growth rings on vertebral centra stained with silver nitrate were employed to back-calculate lengths at ages for the full range (69–328 cm). Our interpretation was based on the hypothesis that two rings are formed on the centrum each year; these age estimates agreed well with results from other methods. Males and females had a similar growth rate even though females grow much larger than males. The oldest female in the sample was 11.5 yr at 328 cm. The oldest male was 4.5 yr at 225 cm. The von Bertalanffy asymptotic growth function adequately described shortfin mako growth: male $L_\infty = 302$ cm, $K = 0.266$, $t_0 = -1$; female $L_\infty = 345$ cm, $K = 0.203$, $t_0 = -1$.

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L'âge et le taux de croissance de mako à nageoires courtes, *Isurus oxyrinchus*, capturés à la ligne et hameçon entre 1961 et 1981 ont été déterminés par quatre méthodes : (1) l'analyse temporelle des données longueur-mois, (2) les résultats de marquages, (3) l'analyse des fréquences de longueurs et (4) les comptages d'anneaux sur les vertèbres. Une analyse temporelle des données longueur-mois établissant la relation entre la taille à un âge donné de sujets de longueur inférieure à 150 cm longueur à la fourche (*FL*) a servi à déterminer la taille (60–70 cm *FL*), l'époque de la naissance (tard au printemps) et les taux de croissance du début (50 cm/an pour les âges 0–I, 32 cm pour les âges I–II). La précision des autres méthodes a été vérifiée à l'aide de ces taux de croissance. Les taux de croissance annuels ont été calculés à partir des retours de marques de 32 mako. Portés sur graphique, ces retours ont donné une courbe de croissance. Les modes des fréquences de longueurs ont permis d'estimer par extrapolation les âges des sujets intermédiaires. Des rétrocalculs de longueur à un âge donné dans la gamme complète de tailles (69–328 cm) ont été effectués sur la base du nombre d'anneaux sur les centres vertébraux colorés au nitrate d'argent. Notre interprétation reposait sur l'hypothèse qu'il se forme deux anneaux annuellement sur le centre : ces estimations d'âge s'accordent bien avec celles obtenues par d'autres méthodes. Mâles et femelles croissent au même rythme, bien que les secondes atteignent des tailles de beaucoup supérieurs à celles des premiers. La femelle la plus âgée dans les échantillons comptait 11,5 ans à 328 cm. Le plus vieux mâle était âgé de 4,5 ans à 225 cm. La fonction de croissance asymptotique de von Bertalanffy décrit adéquatement la croissance du mako : mâles $L_\infty = 302$ cm, $K = 0{,}266$, $t_0 = -1$; femelles $L_\infty = 345$ cm, $K = 0{,}203$, $t_0 = -1$.

Received November 17, 1982
Accepted July 5, 1983

Reçu le 17 novembre 1982
Accepté le 5 juillet 1983

THE shortfin mako, *Isurus oxyrinchus*, is an important member of the pelagic community in temperate waters of the world ocean, yet most details of its life history, including age and growth information, remain undescribed. To be most effective, estimates of age should be validated by relating them to direct observations of growth in time. "Known age methods" include captive rearing and tag-recapture growth studies (Lagler 1956). Holden and Vince (1973) validated their determination that vertebral rings of *Raja* were annual by using injected tetracycline to mark the centrum edge at tagging. We have formulated a "known age method" for young makos based on observations of monthly growth in length and

[1]MARMAP Contribution MED/NEFC 82-3.

Printed in Canada (J7126)
Imprimé au Canada (J7126)

weight. It is one of four methods used to determine age in the shortfin mako: a temporal analysis of length data and tag–recapture data provides direct evidence of juvenile and intermediate growth, while length–frequency analysis and vertebral ring interpretations extend our age determinations through the full range of mako body lengths (69–328 cm).

Several authors have used tag–recapture information to determine or support their determinations of elasmobranch growth (Steven 1936; Holland 1957; Hansen 1961; Holden 1972; Thorson and Lacy 1982). Olsen (1954) used school shark, *Galeorhinus australis*, recapture growth data to support length–frequency derived estimates of age.

Length–frequency interpretation, despite inherent problems, has become a major tool for ageing fish populations. The cornerstone of analysis is the method introduced by Petersen (1892) in which modes are subjectively assigned to age classes. This technique was applied to porbeagles, *Lamna nasus*, by Aasen (1963) and to the school shark, *Galeorhinus australis*, by Olsen (1954). Harding (1949) and Cassie (1954) presented a graphical method for dissecting modes from frequency distributions using probability paper; however, in any but the most clearcut examples, the inflection points in the cumulative frequency line are quite ambiguous for larger sizes.

With the recent proliferation of automatic data processing equipment and its paladins, there have emerged a number of mathematical solutions for frequency data (Hasselblad 1966; Tomlinson 1971; Yong and Skillman 1975; MacDonald and Pitcher 1979).

Elasmobranch skeletal structures have received attention as a source of age information since Kaganovskaia (1933) attempted to estimate the age of the spiny dogfish, *Squalus acanthias*, using dorsal spines. The vertebral centrum is the only other structure known to reflect cyclic marks in elasmobranchs. Whole centra have been used by Daiber (1960), Taylor and Holden (1964), Stevens (1975), and Cailliet et al. (1983). Internal surfaces of cut centra have been polished and studied by Lawler (1976), Tanaka et al. (1978), and Gruber and Stout (1983) or prepared histologically by Ishiyama (1951), Hoenig (1979), Casey et al. (1983), and Schwartz (1983). The objective of our paper is to determine the age and growth of the shortfin mako using the above techniques or modifications of them.

This study was carried out as a contribution to the MARMAP program of the Northeast Fisheries Center and is concerned with defining the role of pelagic sharks in the shelf ecosystem off the northeast coast of the United States.

Materials and Methods

Data used for length–month analysis and the size–frequency distributions were obtained from total catches of shortfin makos at sportfishing tournaments from New Jersey to Rhode Island and from cruises aboard research and commercial longlining vessels (1965–81). Cruise data include measurements of weight, length, and sex determination of sharks collected from Cape Hatteras, NC, to the Grand Banks in nearly all months of the year. Vertebral samples were also obtained at these locations between 1977 and 1981. Care was taken to include vertebral samples representative of the full range of observed lengths (69–328 cm). Some of the analyses employed assume the population to be of a single stock. We have no evidence to the contrary for shortfin mako. Body fork length (*FL*) was utilized rather than total length (*TL*) because it is an easier and more accurate measurement to obtain. Total length may be converted to *FL* by using a relationship derived from our unpublished data:

$$FL = (a + b)TL$$

where the constants are $a = -1.931$ and $b = 0.929$, with $N = 179$ and $r^2 = 0.99$.

Length–Month Analysis

Length–month analysis is a graphical method used to determine directly the growth of 175 juvenile makos in a size range of 54–175 cm. It was employed by Mackintosh and Wheeler (1929) to describe age and growth from conception to weaning of the blue whale, *Balaenoptera musculus*, another poorly accessible pelagic animal. No growth differences due to sex were noted in makos of this size, thus sexes were combined. The plotted makos fell into three strata or clusters, which were statistically compared, identified as cohorts, assigned ages, and fitted with a regression line.

Tag–Recapture

Data on growth from 40 tag–recaptured makos were obtained from over 800 makos that were tagged by us and by cooperative fishermen in the western North Atlantic, principally between Cape Hatteras and Cape Cod (1961–81), using both "M" dart and roto tags (described by Davies and Joubert 1967). To quantify growth, we tabulated tag–recapture information in 20-cm *FL* groups based on the size at tagging. Growth per month and growth per year were calculated. Only growth per year was used because of the small sample size. Growth per year was analyzed using 20-cm groups. Because the data set was too small to break into 20-cm groups without refining, the following criteria were applied to eliminate exceptional and presumably erroneous growth. We assumed that errors in length estimates were normally distributed; therefore, growth that exceeded the linear mean rate (38 cm/yr) established by length–month analysis by ±38 cm (range = 0–76 cm) was deleted. Negative growth was assumed not to occur in this robust population of makos. Growth rates for the 32 refined recaptures were additively graphed into a growth curve for comparison with other methods.

Length–Frequency

Length–frequency distributions were interpreted using an interactive analog computer, the DuPont 310 curve resolver (Müller 1966). Our approach was to introduce "biological structure," as suggested by Schnute and Fournier (1980), derived from our previous length–month and tagging analyses. The 310 curve resolver has been applied to length–frequencies of squid (*Loligo pealei*) by Macy (1980).

Length–frequency diagrams were examined by sex,

month, and year in an attempt to elucidate model class progressions such as shown by Olsen (1954), deSylva (1957), and others. When arrayed over time, our sample sizes were too small to consistently demonstrate polymodality and peak progression. Consequently, data were discretely grouped by combining June samples (male $N = 448$, female $N = 395$) for all years 1963–81 and solved using the 310 curve resolver, calibrated using normal (Gaussian) curves. Solution sets of normal curves determined after several trials provided consistent results. Areas under the curves that are approximations of the number of makos present in each mode from these primarily New York Bight sharks were also determined by the 310 curve resolver.

Vertebral Rings

Vertebrae for age determination were dissected in the field from the branchial region adjacent to the fifth gill arch (15th–20th vertebrae). At sea the entire column was removed, but at tournaments, due to pressures from anglers, only four or five vertebrae bordering the forward dorsal corner of the peritoneal cavity (approximately 15th–20th vertebrae) were secured through a short ventral incision. The intervertebral ligament was perforated to insure rapid penetration of the fixative. Most were preserved immediately in 10% unbuffered Formalin,[2] a few were preserved in 70% ethanol, and all were later transferred to 70% ethanol. A sample of 109 vertebrae was obtained that covered as wide a range of sizes and sexes as possible. The 15th vertebra was processed and "read." When vertebrae were obtained ventrally, the 14th–17th may have been used. Centra in this area are of similar sizes.

Demonstration of Rings on Vertebrae

Several techniques to identify annuli were attempted before an ageing procedure was selected. Transverse vertebral sections were cut with a sledge microtome to include at least one of the radial lamellae (Ridewood 1921). The sections were stained and examined using a technique developed by Casey et al. (1983). This method was unproductive for the shortfin mako. Cyclic zones exist in the exposed lamellae and bordering centrum structures but were indistinct and irregular in location on different vertebrae.

Although all vertebral structures including the connective tissue bear cyclic marks, only the face of each centrum (corpus calcareum) has rings that can be repeatedly located on consecutive vertebrae in the same shark.

Vertebrae from 39 shortfin makos of all sizes were dried and the centrum rings were examined using incident and transmitted light. This method revealed distinct, alternating dark–light bands for young sharks; however, the outer 4–5 mm of the corpus calcareum of larger sharks (over 200 kg) was dense and featureless on dried vertebrae. The above two methods were discarded.

The most satisfactory technique for revealing growth rings on the corpus calcareum was a method using 2% silver nitrate, as described by Stevens (1975). To provide more contrast, the opposite side (corpus calcareum) of each vertebra was removed and the sample was illuminated with strong transmitted light provided by a 150-W fiberoptics light source. The 6-mm fiberoptics light pipe was placed within 5 mm of the cut vertebra. Alternating bands of yellow and dark brown (Fig. 1) can be measured easily with a 10× dissecting scope equipped with an ocular micrometer. To better disclose marginal marks on large specimens, we carefully shaved the corpus calcareum with a scalpel to eliminate surface ridges and valleys before silver nitrate staining. The underlying marks are usually quite clear to the edge of the centrum (Fig. 2). This technique was applied to the full sample of 109 vertebrae.

Slopes of growth estimates of male and female back-calculations and length–frequencies were tested for homogeneity using an analysis of covariance. This test was also applied to the composite growth curves by fitting a linear regression to each curve and then testing for homogeneity.

We attempted to validate the marks used for back calculation as year marks by using information from four tagged makos from which vertebrae were obtained at recapture and processed. The back-calculated size (ring) nearest the *FL* at tagging was determined. The number of vertebral rings should coincide with years at liberty if the rings are annual.

Results

Length–Month Analysis

Length at capture of 175 juvenile makos was plotted against month of capture (Fig. 3). A February embryo reported by Depperman (1953) is included. Cluster analysis using weight at capture as an additional variable determined the stratified groups to be discrete. Based on this evidence and the trend of increasing sizes through the year, especially in the lower cluster, we considered these clusters to be cohorts. Discriminant analysis confirmed these choices. Ages were then assigned as follows. Since size at birth (63 cm) (Stevens 1983) was very close to our smallest free-swimming makos (May $\bar{X} = 73$ cm), this cohort of presumably young-of-the-year makos was assigned to age 0. The second cohort centered around 118 cm was assigned to age I (defined as the first complete year of life, January–January). The last and least distinct cohort due to differential growth was assigned to age II. These clusters may be extended on a continuous 3-yr time axis (Fig. 3) and used to regress a growth curve of early growth for the mako. Predicted size in June (Table 1) for each age was calculated for comparison with other methods. Rate of growth is 49 cm/yr during the 1st yr of life and 32 cm/yr in the 2nd yr (June data, Table 1). Growth of young makos based on these data is best described from 60 to 180 cm by the following equation:

$$FL = 31.38M^{0.46627}$$

where FL = fork length (centimetres), M = month of life, correlation coefficient $r^2 = 0.99$, and $N = 175$.

Tag–Recapture

Tag–recapture information from 40 shortfin makos evi-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIG. 1. Shortfin mako vertebral centrum with connective tissue removed, stained with silver nitrate, and illuminated with transmitted light.

denced considerable variability due mostly to measurement error by sportfishermen on short-term recaptures. Growth rates as high as 161.2 cm/yr and as low as −144.3 cm/yr occurred within these data; an overall mean of the ungrouped growth rates of all 40 recaptured makos was 25.32 cm/yr (SD = 41.23 cm). One 125-cm mako, measured exactly by the authors, grew at the rate of 35 cm/yr over 483 d at liberty.

After refinement by deleting exceptional growth, the remaining 32 makos show a reasonable growth rate diminishing slightly with increasing size (Table 2). Growth rates from 32 refined mako recaptures in 20-cm groups were additively graphed into a growth curve by constructing a series of growth per year right triangles (Fig. 4). The *x*-axis side of each triangle represents 1 yr and the *y*-axis side becomes growth per year for each 20-cm group. Because these *x* and *y* quantities have an angular direction (90 and 360°) they may be treated as vectors and added. The resultant hypotenuse (additive growth vector) becomes a growth curve segment. Since

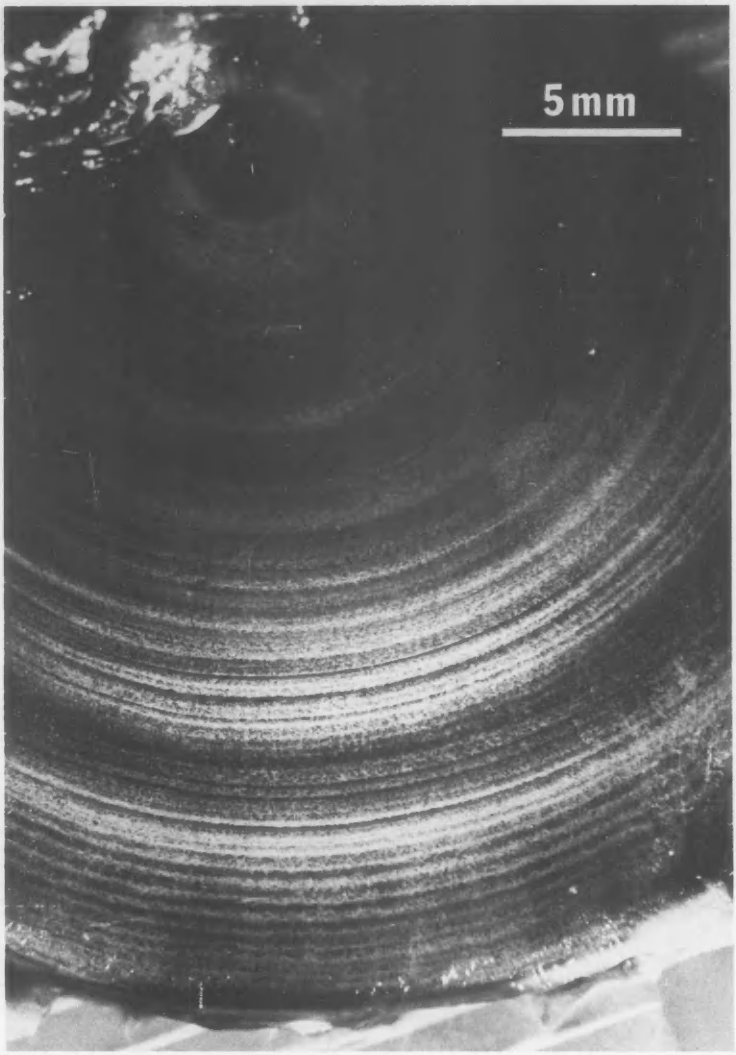

FIG. 2. Shortfin mako vertebral centrum with outer layer of corpus calcareum removed, stained with silver nitrate, and illuminated with transmitted light.

the rate of growth only applies to a discrete range, the portion of the hypotenuse above this range was disregarded (broken line, Fig. 4). To combine curve segments (triangles), the point at which each segment intersects the adjacent 20-cm range becomes the point of origin for the next curve segment. This was continued until all six rates formed a continuous growth curve.

The curve determines rate of growth (slope) and for comparative purposes needed to be positioned on the time axis. Size at age I (121 cm), determined by length–month analysis, provided a point of origin (x,y coordinate) for tag–recapture curve construction.

The graphical analysis of tag–recapture predicts fork lengths for the following ages: birth = 66 cm, 0 = 72 cm, I = 121 cm, and II = 153 cm.

LENGTH–FREQUENCY

Fits with the DuPont 310 curve resolver were obtained

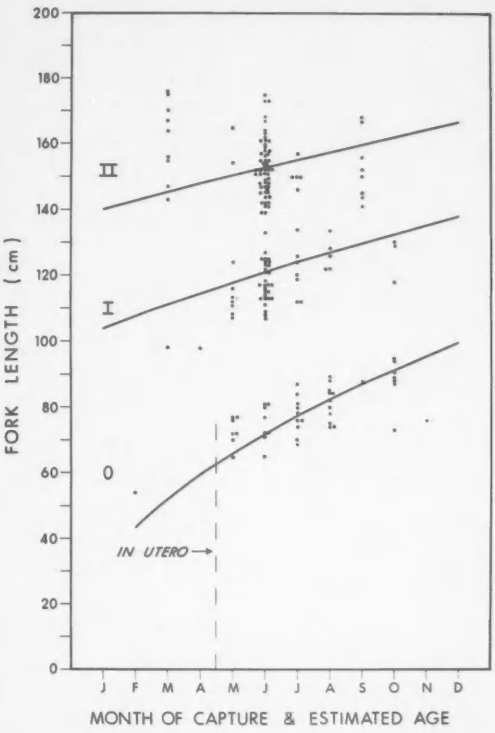

FIG. 3. Length–month diagram of juvenile (age 0–II) shortfin makos with fitted growth curve based on cluster analysis. The *x*-axis is month of capture for the plotted sharks and estimated age for the fitted line.

TABLE 1. Mean size in fork length (cm) of juvenile shortfin mako sharks (ages 0, I, and II) from length–month analysis.

	0	I	II
April	60	114	148
May	66	118	151
June	72	121	153

using eight modes for the males and nine for the females (Fig. 5). For clarity, the intermediate solution line (frequency envelope) that models the population is not shown. It follows the length–frequency line closely and overlays the peaks exactly.

The modal age classes under the right half of each distribution are shifted to the right relative to the frequency envelope and corresponding peaks due to overlap with the right tail of the second major modal class.

Modal means were determined graphically and agreed well between males and females analyzed separately using a *t*-test (significant at the 95% level) (Table 3). The combined sexes

TABLE 2. Growth rates of 32 shortfin mako sharks grouped by size at tagging.

Fork length at tagging (cm)	*N*	At liberty (yr), $\bar{X}$	Growth (cm/yr) $\bar{X}$	Growth (cm/yr) SD
60–80	1	0.3	40.2	—
100–120	1	1.1	38.1	—
120–140	17	1.1	33.4	12.75
140–160	8	1.6	30.9	25.22
160–180	4	1.2	31.0	30.72
180–200	1	0.3	26.0	—

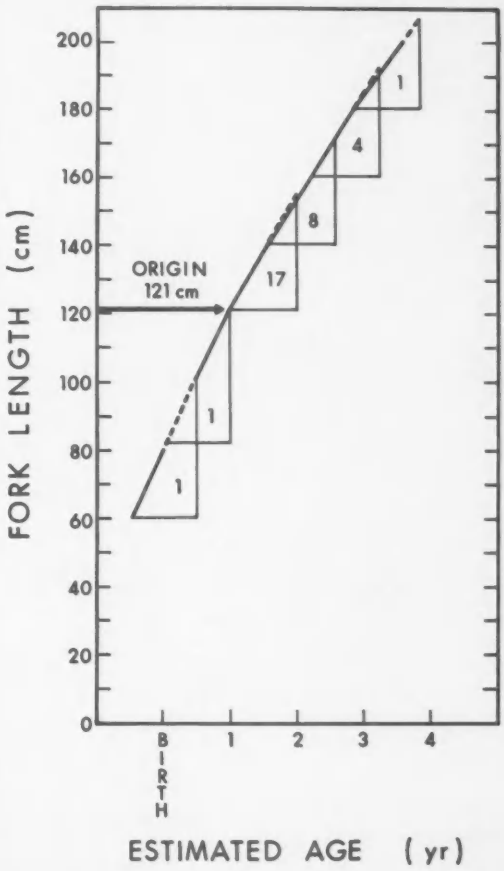

FIG. 4. Growth rates from 32 mako recaptures in 20-cm groups, additively graphed into a growth curve by constructing a series of right triangles. The *x*-axis side of each triangle represents 1 yr and the *y*-axis side is growth per year in each 20-cm group. The hypotenuse is the growth vector and curve segment. Numbers in triangles refer to the number of sharks contributing to each line segment.

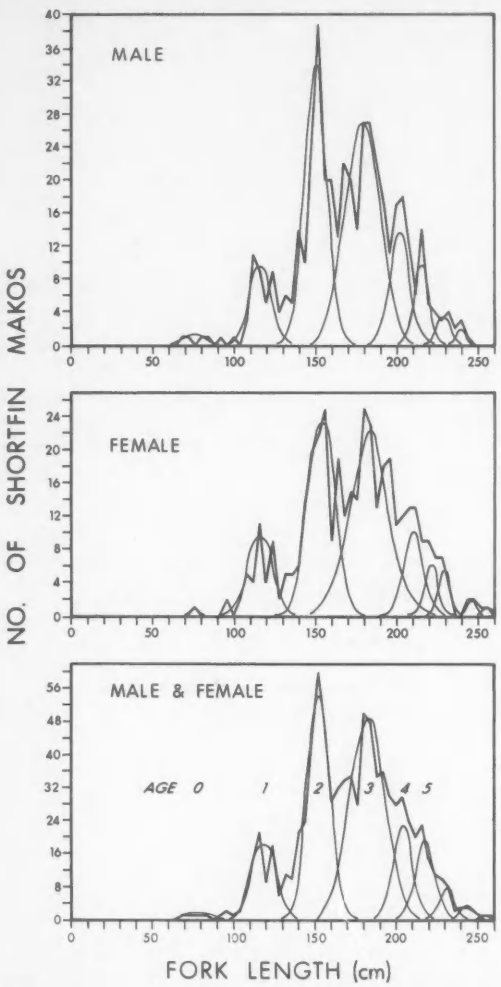

FIG. 5. Length–frequency polygons of fork length versus number of makos caught in each June from 1961 to 1981 with normal (Gaussian) curves overlaid to represent year class modes (see Table 3 for modal means). Males, $N = 448$; females, $N = 395$; males and females, $N = 848$; $i = 4$.

yielded mean values. Modal class size was also determined by the 310 curve resolver.

VERTEBRAL RING ANALYSIS

The fork length vertebral radius relationship was slightly curvilinear (males $r^2 = 0.99$; females $r^2 = 0.99$) (Fig. 6). The data were transformed to account for this. The formula (Rounsefell and Everhart 1953) used for back-calculation was

$$FL = cVR^n$$

where FL = fork length (centimetres), VR = vertebral radius (millimetres), and c and n = constants derived from the data.

Back-calculated size at ring estimates for males and females are in close agreement (significant at the 95% level), but when compared to age estimates from our previous three analyses they indicate growth at approximately one-half the calculated rates. As a result, back-calculated sizes were assumed to be half-year marks (two rings per year) based on results of the three previous methods and given appropriate age assignments (Table 4). When plotted together (Fig. 7), results of the four methods now agree closely. An analysis of covariance for homogeneity of slopes for these four curves was significant at the 95% level.

Growth models were fitted to the back-calculated vertebral data using the nonlinear Biomedical Computer Program BMD PAR. Slight inflections in a Ford–Walford line suggested use of the Gompertz model; however, examination of length–month and length–frequency results indicated these inflections to be artifactual. A von Bertalanffy (1938) model was more descriptive after the first pair of points had been deleted (Fig. 8). Growth curves were fitted for each sex. When the program was permitted to fit all parameters there was poor agreement of t_0 for the two sexes: males = −0.83 yr, females = −2.41 yr. Since young free-living males and females grow at approximately the same rate (Table 3) and are born at a similar size, they most likely grow at the same rate in utero. A t_0 of −1, approximated from extrapolation of the previous three methods (and consideration of Holden 1974) was introduced into the program and the following parameters were generated: males $L_\infty = 302$, $K = 0.266$, $t_0 = -1$; females $L_\infty = 345$, $K = 0.203$, $t_0 = -1$.

The vertebrae from four recaptured makos gave inconclusive results. Two supported the hypothesis that an annual ring is formed. The other two indicated that two rings were formed each year. Validation from this technique must await additional samples.

Discussion

Our approach to shortfin mako age and growth begins with two methods, which, although limited in scope, provide a basis for verifying the interpretation of the more complete traditional methods. As this procedure leads to the assumption of two vertebral rings per year, comparison and integration of these methods are essential in achieving an accurate understanding of mako age and growth.

LENGTH–MONTH ANALYSIS

The length analysis based on monthly increments of growth provides an observational method of demonstrating early age with a limited amount of data. It is applicable because young makos grow rapidly in length and weight. If monthly samples of small makos were available, monthly or seasonal frequency modal class progressions could also be constructed. Small (age 0) makos either are not very susceptible to conventional fishing gear or occupy an unfished niche in the western North

TABLE 3. Length (cm) at age estimates (yr) from length–frequency analysis of June caught shortfin makos, 1965–81, New York Bight. Class size refers to calculated number of fish in each modal class in June tournament populations.

	0	1	2	3	4	5	6	7	8
♂									
N = 448	79	118	151.5	180	203	216	231	241	—
Class size	4.5	40.3	138.9	172.5	51.5	22.4	6.7	4.5	
♀									
N = 395	76	116	153	183.5	210.5	221.5	229.5	246	255
Class size	5.9	47.4	122.5	162.0	37.5	15.8	15.0	7.9	4.0
♂ + ♀									
N = 848	76	118	152	182	204	217.5	231	244	255
Class size	8.5	84.8	254.4	318.0	84.8	72.1	29.7	12.7	8.7

Atlantic. The growth curve derived from this method related growth to actual time and, with tagging results, verifies the year assignments of the less empirical length–frequency and vertebral ring analyses.

GESTATION TIME

The trend of length progression through time revealed by length–month analysis could only occur if parturition were a seasonal event. The appearance of free-swimming juveniles in May at a size slightly larger than Stevens' (1975) estimated size at birth (63 cm) suggests a late spring parturation.

Length–month information can also provide a rough estimate of gestation time (t_0) if intrauterine growth is assumed to be similar to the growth of the young makos analyzed in Fig. 3. Extrapolation of data points to the x-axis yields an estimated t_0 of a little over 1 yr. Known t_0 values in sharks ranges from 6 mo to 2 yr (Holden 1974). Although little is known about lamnid reproduction, 1 yr is a reasonable estimate of t_0 for mako sharks and supports the estimation of t_0 assumed in the growth model.

GROWTH FROM TAGGED SHARKS

Growth rates from tag data based on size estimates from cooperative fishermen are prone to errors through possible over- and under-estimation at both tagging and recapture. In only one case was a mako measured exactly in body length at tagging and recapture. Tag–recapture growth information is limited (40 recaptures). When refined and grouped into one function, a relationship emerges that can be independently compared with results from other methods.

Growth rates are very similar to those determined using the length–month analysis. The only double-measured mako fit the model exactly. Errors of measurement rather than differential growth probably account for the large standard deviations. Holland (1957) speculated that slow growth in tagged spiny dogfish, *Squalus acanthias*, and other fish species is an effect of tagging. When methodologies are compared (Fig. 7) it does not appear that makos are adversely affected by tagging; however, additional recaptures are needed to be certain.

LENGTH–FREQUENCY

From comparison of length and weight frequency curves, it was apparent that the shortfin mako, like most teleosts, reflects environmental and biological effects in its body weight (Ricker 1979). Length–frequencies were chosen for analysis, as they better revealed modes.

By grouping several years of data, shortfin mako length–frequency distributions display adequate polymodality for mode dissection.

The shapes of the length–frequency distributions reflect the availability of makos to June sportsfishermen, possibly due to immigration, emigration, mortality, and selectivity of sportfishing gear. Few makos less than 1 m long are caught and very large sharks (greater than 260 cm) prefer food other than the mackerel and herring baits offered by sportsmen (Stillwell and Kohler 1982) and probably occur elsewhere as a consequence. Makos greater than 260 cm are massive and usually break or avoid sport and commercial fishing tackle. The steep descent of the right edge of the frequency distribution probably is due to mortality, emigration, gear selectivity, or all three.

Double- and triple-peaked modes occur in our mako length–frequency distributions. They are distinctive features and occur repeatedly in subsamples. Interpretation as secondary peaks is justified by their clustering, especially in age I. Growth rates obtained from length–month analysis and tag–recapture results also indicate these to be secondary features.

Speculation on the causes of these peaks may provide clues about the biology of mako sharks. Zero age sharks are caught in June over a wide range of sizes (65–82 cm). These peaks could simply be an artifact of an extended pupping period. Another possible explanation is that some species of large female elasmobranchs give birth to larger young (Holden 1974; Gubanov 1978). Female makos mature at approximately 258 cm *FL* (Stevens 1983). Our results show that sharks of this length are 7 yr old. If maximum size is attained in 11 or 12 yr, there are only 4–5 yr of maturity. Because of senescence, gestation time, or a 2-yr sexual cycle, there may only be two or three litters of increasingly (and uniformly) larger young produced by each female during her lifetime. This hypothesis may explain the occurrence of multiple peaks in the length–frequency modes.

The 310 curve resolver was chosen to resolve length–frequency distributions after trials with more contemporary computer programs such as NORMSEP (Tomlinson 1971), and ENORMSEP (Yong and Skillman 1975) failed to provide

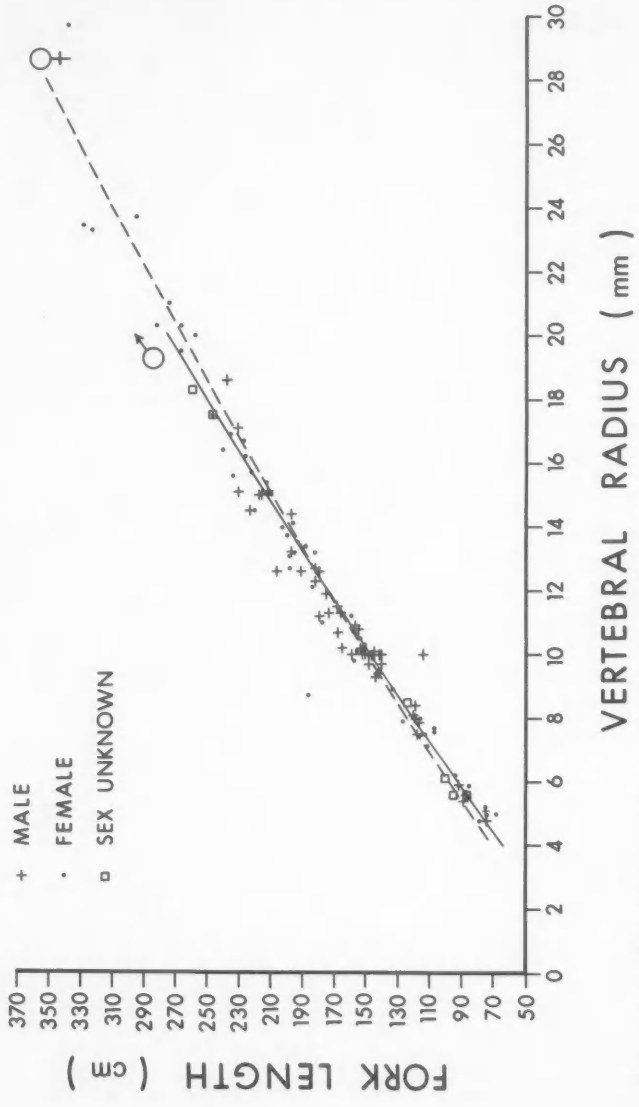

FIG. 6. Shortfin mako fork length–vertebral radius relationship, nonlinear regression.

reasonable estimates of modal means for the partially obscured peaks at ages IV, V, and VI. McNew and Summerfelt (1978) evaluated the original Hasselblad (1966) technique and found that unless there is normality and a very small overlap between peaks, "errors in age composition estimates were generally unacceptable" and "the methodology is not likely to produce a level of accuracy desired for determination of age composition." As noted by Schnute and Fournier (1980), Hasselblad's method may give rise to competing solutions requiring considerable operator introductions of "biological structure into the statistical model to locate solutions of biological interest." We agree with these remarks and prefer the 310 curve resolver because its solutions are interactively determined.

Vertebral Ring Analysis

When converting the vertebral growth curve from one ring per year to two rings per year, assignment of the age 0 ring at 71 cm was governed by the hypothesis that these rings are migration marks (checks). Pups are born in late spring (Fig. 3) in warm temperate latitudes (Depperman 1953; Stevens 1983). The size and location of this ring would coincide with the first migration north from the pupping grounds. Also, assignment at 71 cm is consistent with growth as represented by length−month analysis and tag−recapture growth estimates.

Because of the disparity between length at maturity and maximum sizes of male and female makos, separate vertebral growth information is presented for each sex. As in length−frequency results, there is no significant difference between male and female growth as reflected by back-calculated lengths (Tables 3 and 4), despite the attainment of a much greater size by the females.

The identical growth rates of male and female makos are not apparent in the asymptotic growth curve (Fig. 8). The constant K, the rate at which the growth parameters approach L_∞, is different for males and females (male $K = 0.266$, female $K = 0.202$). This circumstance results from data that are similar (Table 4), projecting very different L_∞ values (male $L_\infty = 302$ cm, female $L_\infty = 345$ cm). The largest measured makos available are our samples at 260 cm *FL* (male) and 328 cm *FL* (female). These L_∞ values are therefore reasonable.[3]

Holden's (1974) K value for *Isurus oxyrinchus* is low compared with our findings. If his data are recalculated using a size at birth of 66 cm and the observed L_{max} of 260 cm for males and 328 cm for females, then the K values become

[3]The largest male we have examined was 260 cm *FL* and 213 kg. John Stevens (CSIRO, Division of Fisheries and Oceanography, P.O. Box 21, Cronulla, N.S.W. 2230, Australia, personal communication) recorded a slightly larger British specimen of 275 cm *FL* and 227 kg (*FL* calculated from weight: wt (lb.) = 0.1792277×10^{-4} (*FL* cm)$^{3.052905}$). Maximum-sized females include four from our data 323−328 cm *FL* and 420−625 kg, an Indian Ocean specimen 350 cm *FL* and 550 kg (Gubanov 1974), and a specimen 324 cm *FL* and 515 kg from California waters (Applegate 1977) (*FL* for the latter two specimens was calculated from weight: wt (lb.) = 0.2786844×10^{-5} (*FL* cm)$^{3.410942}$). These six are the largest makos that, to our knowledge, have ever been reliably measured.

TABLE 4. Back-calculations (cm) of vertebral ring measurements with age assignments.

Sex	N	B	Ring No. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
									Age (yr)				5		6		7		8		9		10		11	
♂	49	70	76	99	122	145	167	185	203	210	220	232														
♀	54	76	84	104	127	149	169	185	196	207	217	226	231	241	249	258	267	274	276	295	306	311	316	320	335	301
♂ + ♀	109	74	81	102	125	148	168	184	197	206	216	226	231	241	250	260	269	276	278	297	309	314	318	323	338	303

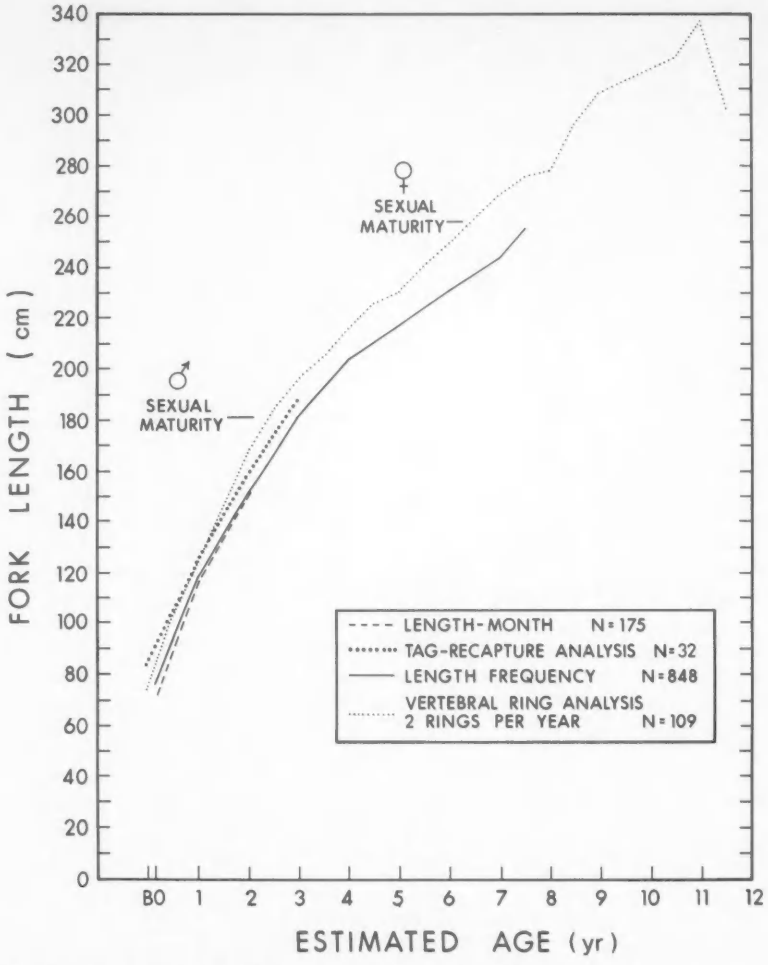

FIG. 7. Composite growth estimates from four methods for shortfin mako.

0.293 and 0.217, respectively. These are higher values than Holden considers typical of Selachii but acceptable for Batoidei and other fast-growing species.

Vertebral rings occur systematically as length increases. Their formation is probably more directly related to factors other than size. In traditional age studies, year marks usually form in winter when growth of the recording structure slows due to the effects of cold. Makos are warm bodied (Carey and Teal 1969) and migrate in waters of a discrete temperature range (17–24°C) (John Hoey, Fishery Biologist, NOAA, National Marine Fisheries Service, Narragansett Laboratory, Narragansett, RI 02882, personal communication). The vertebrae are thus sheltered from environmental temperature extremes. A more likely cause for ring formation would be times of stress or deprivation such as migration and mating. The rings would then only be related to time when yearly migrations are undertaken and not occur regularly in all individuals (i.e. those that do not migrate very far). Vertebral rings may thus yield an approximation of age, accurate in the smaller sizes where estimates have been correlated with other methodology. Adults may not lay down yearly rings, and it is possible that we have underestimated their age, but we have no data to support this possibility.

Parker and Stott (1965) determined that the basking shark, *Cetorhinus maximus*, like the mako, forms two vertebral rings (concentric lamellae) per year. There is a scarcity of information on the basking shark's winter habits. Pauly (1978) disputes the two rings per year theory citing references (Muus

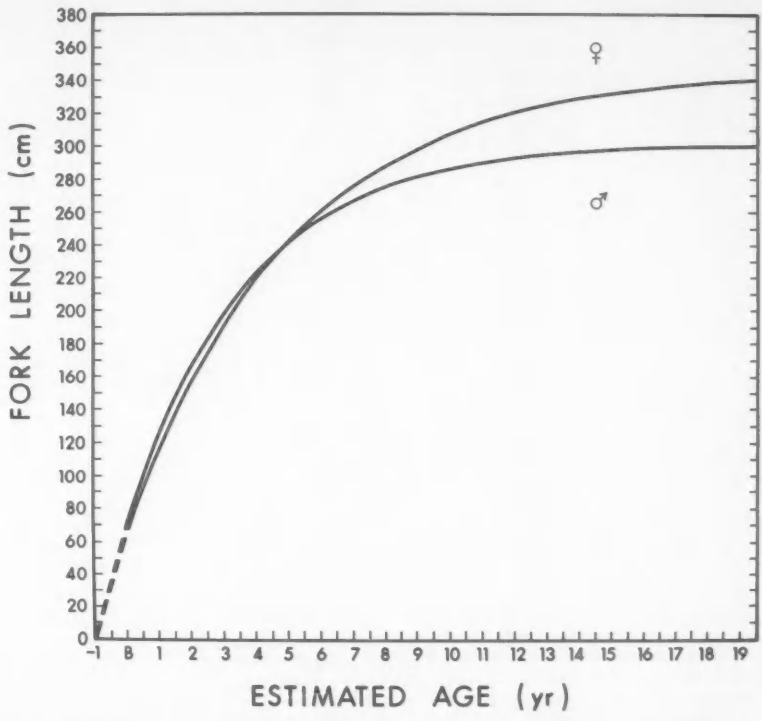

FIG. 8. von Bertalanffy growth curves of male and female makos based on back-calculations (Table 4) assuming two rings per year. Male L_∞ = 302 cm, K = 0.266, t_0 = −1; female L_∞ = 345 cm, K = 0.203, t_0 = −1.

and Dahlström 1974) that basking sharks hibernate and presumably do not grow 4–6 mo of each year. Since life history information for the basking shark is incomplete and the rings used by Parker and Stott (1965) differ in form, location, and origin from the annulation-bearing corpus calcareum of the mako that we employ, comparison with the basking shark is at this time inconclusive.

The existence of two rings per year in the dorsal spines of tunas has been established (Chi and Yang 1973; Antoine et al. 1983; and references cited within). Couplets or groups of rings may indeed prove to be common in pelagic migratory animals.

Growth of the shortfin mako is rapid when compared with most other sharks. It grows at nearly twice the rate of the porbeagle, *Lamna nasus* (Aasen 1963), and much faster than typical carcharhinid sharks (Casey et al. 1983). Its growth is commensurate with that of other species of pelagic fish such as dolphin (Beardsley 1967), blue sharks (Stevens 1975), tunas, and billfish (International Workshop on Age Determination of Oceanic Pelagic Fishes—Tunas, Billfishes, Sharks, Miami, FL, 15–18 February 1982).

Its rapid rate of growth might make the shortfin mako a candidate for a commercial fishery; however, its low fecundity (Stevens 1983) would limit the fishery's size.

Acknowledgments

We thank the members of the Bay Shore Tuna Club for help at their annual mako tournament. Charles Stillwell and Alan Lintala of the NOAA-NMFS Narragansett Laboratory, and Bob Conklin of Riverhead, NY, helped with specimens and vertebral collections. Mike Couturier and Nancy Kohler provided ADP and statistical support. Sincere thanks to John Stevens of CSIRO, Australia, for data and encouragement and to Bernard Skud, Alex Wild, Saul Saila, Eric Prince, John Hoey, and George Benz for valuable manuscript suggestions.

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Reproductive Potential of Three American Lobster *(Homarus americanus)* Stocks in the Canadian Maritimes

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CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three American lobster *(Homarus americanus)* stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958 – 1967.

New information on female size at maturity, fecundity, and relative egg production per recruit is presented for American lobsters *(Homarus americanus)* from three areas in the Canadian Maritimes. Based on pleopod examination, sizes at 50% maturity for females were estimated at 108.1 mm carapace length (CL) from the Fundy area (Bay of Fundy and southwestern Nova Scotia), at 92.5 mm CL from eastern Nova Scotia, and at 78.5 mm CL from Northumberland Strait. There was a curvilinear relationship between the number of eggs per female and CL. An egg-per-recruit model predicted that in all three areas the second and third molt groups beyond the legal minimum recruit size contribute the most to egg production under current exploitation rates. Lobsters in Northumberland Strait and eastern Nova Scotia produce up to 30–50% of their eggs at sizes smaller than those at which females from the Bay of Fundy start to produce eggs. Although the stock–recruitment relationships for *H. americanus* are unknown, the egg-per-recruit assessment suggests that all three areas would benefit in egg production increases by increasing minimum legal recruit size by one molt increment.

CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three American lobster *(Homarus americanus)* stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958 – 1967.

On trouvera dans l'article qui suit des données nouvelles sur la taille des femelles à la maturité, la fécondité et la production relative d'oeufs par recrue de homards Américains (*Homarus americanus*) provenant de trois régions des provinces Maritimes du Canada. Après examen des pléopodes, on estime que la taille à laquelle 50 % des femelles sont matures est de 108,1 mm de longueur de carapace (LC) dans la région de Fundy (baie de Fundy et sud-ouest de la Nouvelle-Écosse), de 92,5 mm LC dans l'est de la Nouvelle-Écosse et de 78,5 mm LC dans le détroit de Northumberland. Il y a relation curvilinéaire entre le nombre d'oeufs par femelle et LC. Un modèle de production d'oeufs par recrue permet de prédire que, dans les trois régions, aux taux d'exploitation actuels, les groupes de seconde et de troisième mue après que soit atteinte la taille minimale légale des recrues sont ceux qui contribuent le plus à la production d'oeufs. Les homards du détroit de Northumberland et de l'est de la Nouvelle-Écosse produisent jusqu'à 30–50 % de leurs oeufs à des tailles inférieures à celle à laquelle les femelles de la baie de Fundy commencent à produire les leurs. Bien qu'on ignore les relations stock–recrutement chez *H. americanus*, une évaluation de la production d'oeufs par recrue donne à penser que les trois régions profiteraient d'une production d'oeufs accrue si on augmentait la taille minimale légale des recrues de l'équivalent de l'accroissement d'une mue.

Received March 17, 1983
Accepted July 6, 1983

Reçu le 17 mars 1983
Accepté le 6 juillet 1983

SIZE at maturity and relative population fecundity are important characteristics for assessment modeling of exploited species such as the American lobster, *Homarus americanus* (Caddy 1977, 1979; Ennis and Akenhead 1978). Current

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Printed in Canada (J7302)
Imprimé au Canada (J7302)

reviews of the extensive literature on lobster reproductive biology (Aiken and Waddy 1980a, 1980b; Ennis 1980; Van Engel 1980) indicate a lack of detailed information on the reproductive potential of American lobsters. In addition, a recent Canada–U.S. Workshop (Anthony and Caddy 1980) recognized the need for research on fecundity and size at maturity relationships of lobsters around the Canadian Maritimes.

Although there is no definitive information to indicate genetically discrete *H. americanus* populations (Barlow and Ridgway 1971; Tracey et al. 1975), analysis of commercial landing trends suggests that there may be at least three lobster stocks in the Canadian Maritimes: the Bay of Fundy area (including the Bay of Fundy and southwestern Nova Scotia), the southern Gulf of St. Lawrence, and the south and eastern or Atlantic coast of Nova Scotia (Campbell and Mohn 1983; Harding et al. 1983). For our purposes we use Ricker's (1975) definition of a stock as being that part of a population that is under consideration from the point of view of actual or potential utilization. Despite high exploitation rates (Paloheimo 1963; Campbell 1980), lobster landings in most of these areas have been relatively stable for the past 30 yr, with a few exceptions such as along the eastern shore of Nova Scotia and central Northumberland Strait where commercial landings have declined in recent years (Campbell and Mohn 1983).

During the past decade, biologists and fishermen have expressed concern that the Canadian lobster fishery has been overharvested and, consequently, landings and revenues have been reduced (Robinson 1979). Present management regulations include limits on the number of licensed fishing vessels and traps per fisherman, protection of egg-bearing females, recruit size limits, and fishing season restrictions. Biologists have advocated increases in minimum legal size (recruit size) as the most effective conservation measure for most lobster populations in the United States and Canada (Anthony and Caddy 1980). Acheson and Reidman (1982) found that the economic value of the lobster fishery in Maine would increase with increases in recruit size under current fishing mortalities. There are few yield-per-recruit analyses (Ennis 1980) and no egg-per-recruit analyses available for lobsters in Canada.

For each area, a combination of different factors may affect the total number of eggs per recruit that a lobster can produce. These factors may include the timing of fishing season, recruit size, fishing mortality, size at maturity, and growth rate. Managers are interested in the effect of these factors on lobster reproductive potential. We present analyses of female size at sexual maturity, fecundity relationships, and an egg-per-recruit model that examines the relative egg production under various recruitment sizes and fishing mortalities of lobsters from Northumberland Strait, the Bay of Fundy, and off the east coast of Nova Scotia (Fig. 1).

FIG. 1. Sampling areas in waters off Nova Scotia, New Brunswick, and Prince Edward Island. The three general areas referred to in this paper are Bay of Fundy area (Grand Manan to Seal Island), eastern Nova Scotia (Port Mouton to Gabarus), and Northumberland Strait (Escuminac to Murray Harbour).

Materials and Methods

SIZE AT SEXUAL MATURITY

Estimating sexual maturity involved examining pleopods for well-developed cement glands (stages 3 and 4) (Aiken and Waddy 1982), which indicate that egg extrusion is imminent. This method allowed differentiation of nonovigerous females as those that would and those that would not extrude eggs during the current spawning season. The proportion of nonovigerous females with well-developed cement glands in the total female catch was estimated from at least 30 per 5-mm carapace length (CL, millimetres) class intervals from trap-caught lobsters in Northumberland Strait (Murray Harbour and Lismore) during June–August 1978, from the eastern shore of Nova Scotia (Gabarus, Fourchu, and New Harbour) during July–August 1978, and the Bay of Fundy (Grand Manan) during July–August 1982. Data from various locations were combined to represent the three general areas for convenience in further analyses.

The relationship between CL (X) and the proportion of sexually mature females (Y) by 5-mm CL groups was approximated by using a sigmoid function:

$$Y = \frac{a}{1 + e^{b+cX}}$$

where a, b, and c are empirical constants estimated by nonlinear least squares approximation, using Marquardt's algorithm (Marquardt 1963; Conway et al. 1970).

FECUNDITY

All external eggs were removed from each ovigerous female and preserved in 5% formalin solution for ≥ 24 h. A subsample of 10–15 preserved eggs was taken and the

longest and shortest axes of the darkly pigmented crescent of the eye of each egg were measured to the nearest 0.01 mm; the two measurements were averaged to obtain the eye index, a measure of egg development (Perkins 1972). All preserved eggs were then oven-dried at 70°C for 48 h, and the dried egg mass was rubbed over a screen sieve (0.250 mm) to separate the eggs from extraneous material. The total egg mass was weighed and eggs in three weighed subsamples were counted to estimate the total number of eggs per female (including the number of eggs removed for the eye spot index measurements). Error associated with this method was estimated at <1% when compared with counting the total number of eggs from five females. Due to a loss of eggs during incubation (Perkins 1971) the total number of eggs per female was determined only from eggs within 1–2 mo of hatching (400–530 eye spot index range). This corresponds to May–June 1979 for Northumberland Strait (Escuminac, Cape Tormentine, and Murray Harbour) and for east Nova Scotia (Fourchu and Three Fathom Harbour) and July–August 1979 for the Bay of Fundy (Grand Manan, Chance Harbour, and Alma) (Fig. 1). Our estimate of the total number of eggs per female should be considered a minimum because some eggs were probably lost while the lobsters were transported to the laboratory. Female lobsters in the process of hatching their eggs or ones infested by a nemertean worm (Aiken et al. 1983) were not considered for the fecundity estimates.

The relationship between carapace length (X) and the number of eggs per female (Y) was approximated, using a curvilinear equation of the form $Y = aX^b$. After transforming both X and Y by $\log_e$, the empirical constants a and b were estimated by using the linear least squares method. Fecundity estimates for *H. americanus* from different areas in our study and for those of Herrick (1911), Saila et al. (1969), Squires (1970), and Perkins (1971) were compared using analysis of covariance after $\log_e$ transformation of the data from the same size ranges for which data were available.

Egg-per-Recruit Model

An egg-per-recruit model was developed to determine the relative potential number of eggs produced by 1000 female recruits entering a fishery. The following equations are a modification of those developed by Caddy (1977, 1979) and Robinson (1979). The total egg production was determined from the sum of eggs produced from each molt (size) group, m, in the population. The reproductive potential per molt group, m, is expressed as

$$(1)\quad E_m = N_m \cdot Pr_m \cdot Ex_m \cdot Fc_m$$

where E_m = total number of eggs (about to hatch) produced in molt group m, N_m = number of female lobsters in m, Pr_m = proportion of sexually mature females in m, Ex_m = proportion of females extruding eggs in m (this "extrusion factor" is a function of the molt condition and the ability of older females to have multiple egg extrusions within an intermolt period (Aiken and Waddy 1980a, 1980b)), and Fc_m = fecundity of females in m at time of hatching of eggs or fecundity of females at time of egg extrusion multiplied by survival of eggs during incubation.

Values for E_m are accumulated from each molt group, and the total egg production (E_t) for all molt groups is

$$(2)\quad E_t = \sum_{m=1}^{\max} E_m$$

where max is the molt group of the largest sized lobsters.

The number (N_m) of female lobsters surviving and molting into another size group was approximated by modifying Caddy's (1979) formula to include multiple extrusion:

$$(3)\quad N_m = N_{(m-1)} \cdot e^{-F(\Delta t_m - te_m \cdot Ex_m \cdot Pr_m) - M \cdot \Delta t_m}$$

where Δt_m = intermolt period (years) for molt group m, te_m = external egg-bearing or incubation period (years), F = annual instantaneous fishing mortality rate (ovigerous females excluded), and M = annual instantaneous natural mortality rate.

The formula takes into account the period of external egg incubation when fishing effort is not applied to trapped ovigerous females, which must be returned unharmed to the sea (due to berried female law). The external egg-bearing period, te_m, of 1 yr was assumed for all areas, although te_m may vary from 9 to 12 mo, depending on geographic and seasonal variations in temperature affecting the duration of egg incubation and the timing of the molt cycle, ovary development, and egg extrusion. The length of the egg-bearing period within a molt group is also affected by the proportion mature, Pr_m, and proportion of lobsters extruding eggs more than once per intermolt period.

The computer program developed by Caddy (1979) was adjusted to accommodate the above formulae and run to obtain the relative egg production after using the appropriate reproduction and growth parameters for each area studied. We assumed that trap selectivity or retention was constant (1.0) for all size groups to simplify analyses for this paper. The relative population fecundity under a given fishing regime included the number of eggs produced for all mature females in both prerecruit and recruit sizes. A more detailed explanation of the model can be found in Caddy (1977, 1979). Recruit size is the minimum legal size in the fishery.

The input parameters used in the egg-per-recruit model were as follows. Growth rates expressed as two components, molt increment and proportion molting, were determined from tag–return data where size at release and recapture of lobsters were known (Table 1). The intermolt period (Δt_m) was calculated as the reciprocal of the proportion molting for each CL. Proportion mature (Pr_m) was obtained from the maturity ogives (Fig. 2; Table 1). Extrusion factor (Ex_m) was considered as being 1.0 at values of $Pr_m \leq 1.0$ and thereafter half of the intermolt period, Δt_m, up to approximately 2.0 at about 170 mm CL; the simulations generally terminated at 170–180 mm CL. The equation for overall size–fecundity (Fc_m) relationship was used for all three areas for convenience, as the intercept of the equation was found to be not significantly different from that for each of the three areas. The value of M was assumed to be 0.10. Values of M are normally difficult to determine for lobsters, although some studies have found M to range from 0.02 to 0.35 (Thomas 1973; Campbell 1980).

TABLE 1. Size at maturity and growth parameter values for female lobsters used in the egg-per-recruit simulations. Correlations for the growth equations are significant at $P < 0.01$. CL (X) = carapace length (mm), SE = standard error of estimate, R = correlation coefficient.

Equations and details	Bay of Fundy	Eastern Nova Scotia	Northumberland Strait
Proportion mature = $\frac{a}{1 + e^{b+cX}}$			
a	1.00	1.00	1.00
b	23.23	10.40	20.48
c	−0.214	−0.112	−0.261
SE	0.016	0.037	0.017
Postmolt CL (X) = aX^b			
a	2.107[a]	1.693[b]	1.837[c]
b	0.864	0.907	0.892
R	0.988	0.994	0.982
CL range	60−153	62−91	55−80
Proportion molting = ae^{bX}			
a	1.9500[a]	2.6332[b]	2.2195[c]
b	−0.0097	−0.0139	−0.0122
R	0.934	0.939	0.980
CL range	61−143	62−90	50−85

[a]Campbell 1983.
[b]Gabarus, N.S., 1958−59 (D. G. Wilder, unpublished data).
[c]Egmont Bay, P.E.I., 1954−55 (Wilder 1963) combined with Murray Harbour, P.E.I., 1978 (D. G. Robinson, unpublished data).

Results

Size at Sexual Maturity

The maturity curves indicated that 50% maturity occurred at 108.1 mm CL for the Bay of Fundy area, 92.5 mm CL for the eastern shore of Nova Scotia, and 78.5 mm CL for Northumberland Strait (Fig. 2; Table 1). The size-at-maturity data from the eastern shore of Nova Scotia show a transitional size at maturity between the Fundy area and Northumberland Strait. Female lobsters in waters of both the Bay of Fundy and Northumberland Strait have an approximate 40-mm CL range in transition from functional 0−100% maturity, whereas along the eastern Nova Scotia shore this size range is about 60 mm CL.

Onset of size-at-maturity ogives (Fig. 2) matches well with presence of the smallest ovigerous females observed in 10 000 lobsters sampled at sea during 1977−80 in these areas. The smallest and largest ovigerous females caught were 85 and 188 mm CL in the Bay of Fundy, 68 and 166 mm CL in eastern Nova Scotia, and 60 and 142 mm CL in Northumberland Strait.

Fecundity

There was a curvilinear relationship between the number of eggs per female and CL (Fig. 3). Of the 166 ovigerous females examined for this study, the lowest number of eggs per female was 2186 from a 69-mm CL specimen trapped in Northumberland Strait and the highest was 77 242 from a 146-mm CL female trapped in the Bay of Fundy. Herrick (1911) recorded the highest value to date of 97 440 eggs for a 141-mm CL *H. americanus* female.

There were no significant differences in slopes or elevations ($P > 0.05$) using analysis of covariance in the size−fecundity relationships for females of a similar size range for locations within each of the general areas studied. Therefore, the data were combined for study sites within each of the three areas: Bay of Fundy, eastern Nova Scotia, and Northumberland Strait (Fig. 3).

We did not compare the fecundity of the smaller females from Northumberland Strait and Fourchu with the larger females of the Bay of Fundy because of the different size groups involved. Instead, we combined the data from all areas to obtain an overall equation

$$Y = 0.00256X^{3.409} \ (N = 166, R = 0.933)$$

and found, using analysis of covariance, that although the slope was significantly different ($P < 0.01$) from the size−fecundity equations for Northumberland Strait and eastern Nova Scotia (Fig. 3B, 3C), neither the elevations of the latter two equations nor the slope and elevation of that for the Bay of Fundy were significantly different ($P > 0.05$) from the overall equation. Whether this slope difference is due to geographic differences or to the lack of data for the larger lobster size group (e.g. 110−140 mm CL) (Fig. 3B, 3C) cannot be determined from available data.

Eggs per Recruit

The simulation results should not be considered in absolute terms, but rather in relative terms for various size groups, as being indicative of the reproductive potential of lobster populations under different fishing mortalities and recruit sizes.

Figure 4 shows the relative contribution to total egg

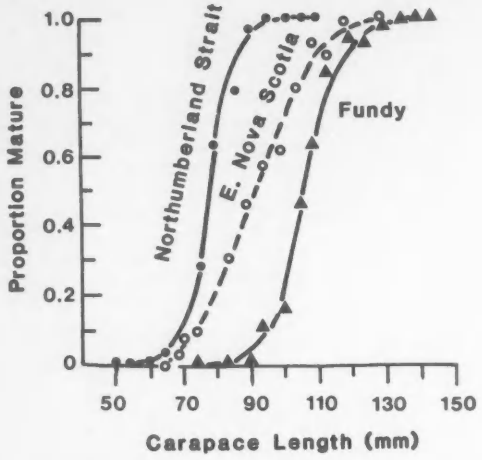

FIG. 2. Maturity curves (Northumberland Strait, eastern Nova Scotia, and Bay of Fundy) based on developed cement glands on pleopods, which indicate that egg extrusion is imminent. See Table 1 for logistic curve constants.

numbers by various sizes of females under ranges of F that were prevalent during 1977–80; mean of F was 1.40 (range 0.43–1.92) for Bay of Fundy, 0.63 (0.54–1.02) for eastern Nova Scotia, and 1.7 (1.51–2.02) for Northumberland Strait (Robinson 1979; Campbell 1980) assuming $M = 0.10$ (Thomas 1973). Many eggs in the other general areas (30–50% for Northumberland Strait and 10–30% for eastern Nova Scotia) were produced at sizes smaller than that at which females from the Fundy area start to produce eggs. The second and third molts or intermediate sizes above recruit size in all areas contribute the most eggs because of the greater number of ovigerous females than in the larger size groups. Even though large females have a greater fecundity, there are fewer lobsters than the smaller, mature females. Most (>70%) of the potential egg production is contributed by the size range of 100–140 mm CL for the Bay of Fundy, 80–130 mm CL for eastern Nova Scotia, and 70–110 mm CL for Northumberland Strait (Fig. 4). This agrees with size range at which the highest proportion (0.10–0.31) of ovigerous to total females per 5-mm CL group was found in at-sea trap sampling of over 10 000 lobsters in these areas during 1977–80; the range was 100–160 mm CL for the Bay of Fundy, 85–130 mm CL for eastern Nova Scotia, and 70–110 mm CL for Northumberland Strait. There is a direct relationship between fishing mortality and egg production; as the F increases (Fig. 4), fewer females reach maturity and the slope of the ogive increases. In contrast, as the fishing pressure decreases, more females reach maturity and/or extrude eggs, causing the ogives to have a lower slope (Fig. 4).

The effect of multiple extrusion was negligible (<5% increase in eggs per recruit) compared with simulations with only one extrusion allowed per intermolt period at $F \geq 1.0$. With $F < 1.0$, however, more females escaped exploitation,

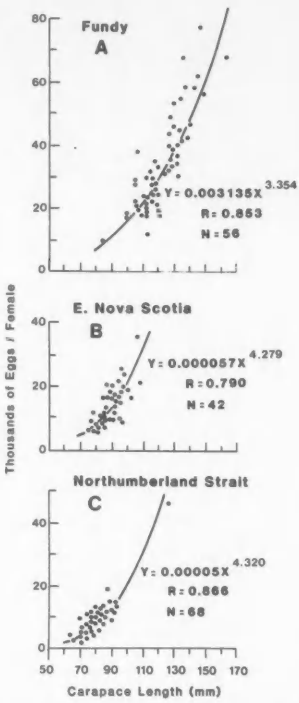

FIG. 3. Fecundity of female lobsters carrying well-developed eggs prior to hatching from (A) Bay of Fundy, (B) eastern Nova Scotia, and (C) Northumberland Strait. N = number of values, X = carapace length, Y = thousands of eggs per female, and R = correlation coefficient.

allowing a greater increase in egg production with multiple extrusions compared with single egg extrusions per intermolt period (e.g. $F = 0.4$ resulted in a 15–25% increase in eggs per recruit).

Figure 5 shows how the relative number of eggs per recruit is sensitive to various fishing regimes and size at recruitment for the three areas. With decreases of F and increases of recruit size, more eggs per recruit would result. At higher F values the effects of size at maturity and size at recruitment greatly influence the difference between areas in the number of eggs per recruit. At lower F values (<0.4) the difference in number of eggs per recruit diminishes between areas. In the Fundy area, the current recruit size of 81.0 mm CL is effectively one molt below onset of egg production and two to three molts below 50% egg production (Fig. 2, 4A). In contrast, recruit size of 81 mm CL along the east shore of Nova Scotia is larger by about one molt than the onset of egg production but still one to two molts smaller than about 30% egg production (Fig. 4B). Egg production per recruit is greater for female lobsters from the eastern Nova Scotia area than that for the Fundy area at equivalent fishing regimes and recruit sizes (Fig. 5A, 5B). The recruit size of 63.5 mm CL

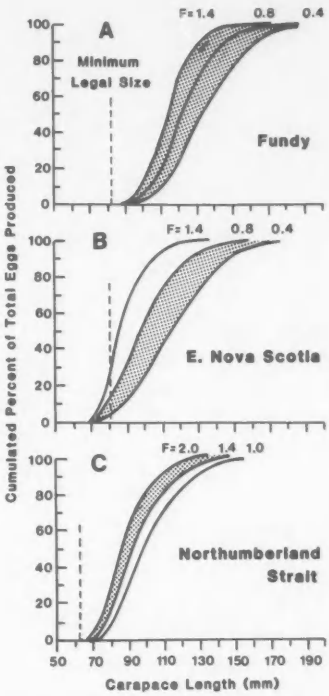

FIG. 4. Relative reproductive potential of female lobsters of different sizes under current fishing regime ranges and minimum legal sizes (= recruit size) in (A) Bay of Fundy, (B) eastern Nova Scotia, and (C) Northumberland Strait, expressed as cumulative percent of total eggs produced. Shaded areas indicate relative egg production under the majority of estimated fishing mortalities from various locations within an area during 1977–80.

for Northumberland Strait is approximately at the onset of egg production and approximately two molts lower than the 50% egg production level (Fig. 4C). Thus, given the present recruit size, the number of eggs per recruit for Northumberland Strait is intermediate between that of the Fundy and eastern Nova Scotia areas (Fig. 5).

Discussion

Our results indicate that lobsters mature at a smaller size in Northumberland Strait than in the Bay of Fundy and that there is a transition in size at maturity between these two areas along eastern Nova Scotia. Differences in size at maturity have been attributed to trends in summer temperatures from one geographic area to another. Templeman (1936) suggested that the negative correlation between summer water temperatures and onset of sexual maturity of female lobsters was a result of differential growth of somatic and reproductive tissues; thus, a female exposed to high summer temperatures matures at a smaller size compared with females living in areas with low summer temperatures. Other factors that probably influence lobster size at sexual maturity are population density, food availability, and photoperiod (Aiken and Waddy 1980a, 1980b).

Our study assumes that seasonal changes in water temperatures and photoperiod force female *H. americanus* to synchronize molting and reproduction to occur usually during summer (June–September). Indeed, annual variations in size at maturity and growth may occur in one area due to climatic changes so that ovarian and somatic growth cycles may become antagonistic under limited temperature regimes. For example, during most years, shallow-water temperatures in western Northumberland Strait are sufficiently high during the summer months to allow almost all prerecruit females to molt twice or molt once and extrude eggs during the same summer (Templeman 1934, 1936; Wilder 1963; Robinson 1979). In cool years the second event is delayed and may occur for only a small portion of the population. Molting and extruding eggs during the same year appear to occur only during the first ovarian cycle for lobster from the Gulf of St. Lawrence and Newfoundland (Aiken and Waddy 1980b; Ennis 1980). A 2-yr ovarian cycle continues throughout most of the reproductive life of mature female lobsters in most other areas, with egg extrusions occurring in alternate years and with molting between successive extrusions (Aiken and Waddy 1980b). However, Campbell (1983) found that about 20% of tagged female lobsters in the Bay of Fundy extruded a second batch of eggs without molting, supporting Aiken and Waddy's (1980b) suggestion that a few large mature females in the wild may have multiple egg extrusions between molts. Considering that intermolt periods may extend ≥4 yr in large female lobsters, notwithstanding the continuation of the 2-yr ovarian cycle, it is conceivable that many large females may undergo multiple extrusions of at least two broods within an intermolt period. Alternating years of molting and mating appear unnecessary, since a female is apparently capable of fertilizing at least two broods from a single insemination (Aiken and Waddy 1980a).

We compared our size–fecundity relationships with published data from other areas (Herrick 1911; Saila et al. 1969; Squires 1970; Perkins 1971) by using analysis of covariance on equivalent sizes and found differences with the published values in elevations ($P < 0.01$) but not in slopes ($P > 0.05$) with our data from Fundy, eastern Nova Scotia, and Northumberland Strait areas. Geographic differences in lobster fecundity have also been shown for Newfoundland (Ennis 1981). Because environmental and biotic (Aiken and Waddy 1980a, 1980b) factors in different geographic areas may influence variation in lobster size-fecundity relationships and possibly year-to-year variation within the same area (Bagenal 1973), we suggest that fecundity estimates be obtained for each lobster population studied.

There are few published data on the relative population fecundity of different species of lobster. Berry (1971) found that the intermediate sizes of mature females of the spiny lobster, *Panulirus homarus* (L.), although producing fewer eggs per extrusion than the larger females, spawned more frequently and thereby contributed the most eggs to the population. Gregory et al. (1982) found that the most productive size class of spiny lobster, *P. argus* (Latreille),

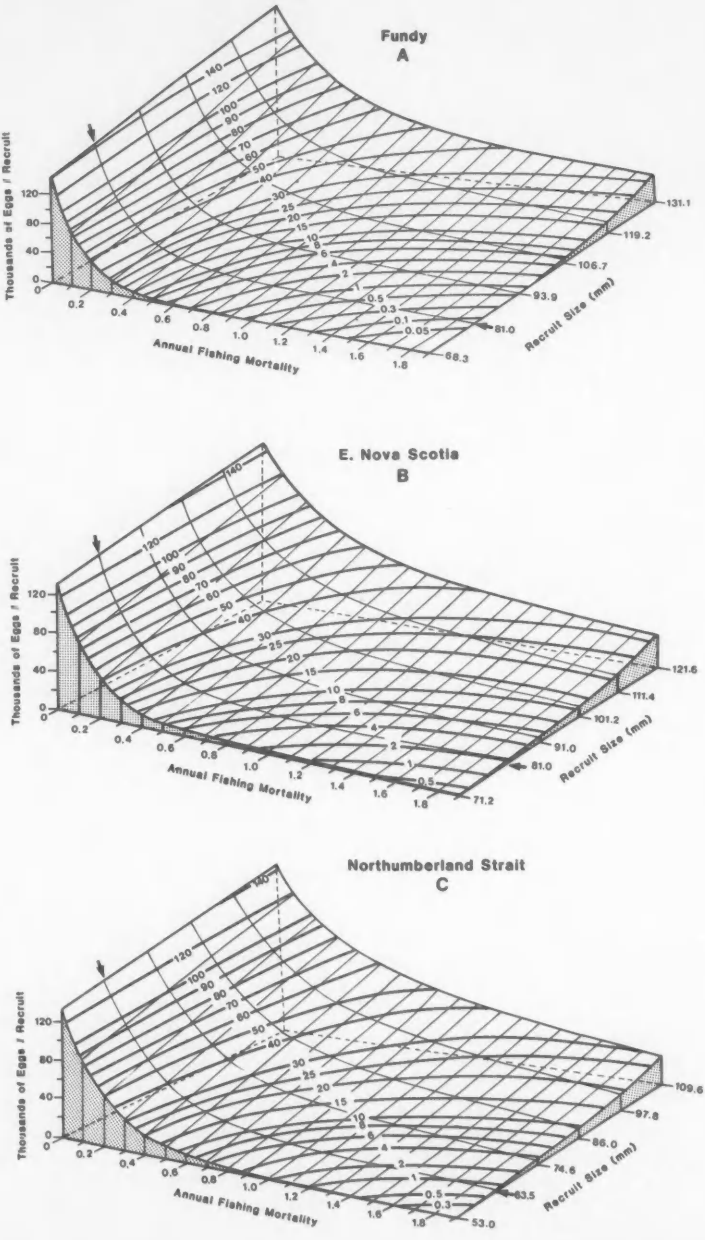

FIG. 5. Three-dimensional graphs indicating relative population fecundity of female lobsters under different fishing mortality regimes and recruit sizes for (A) Bay of Fundy, (B) eastern Nova Scotia, and (C) Northumberland Strait. Arrows indicate current recruit sizes or minimum legal sizes.

consisted of females newly recruited to the fishery (75–85 mm CL), which contributed about half of the total annual egg production. Saila and Flowers (1965) developed a simulation model to predict the total fecundity of an *H. americanus* female population under various exploitation and natural mortality rates and regulations for protecting ovigerous females. They found that protection of large lobsters was not biologically useful because of the small numbers surviving under most exploitation rates. Protection of ovigerous females clearly produces more eggs than females without protection (Saila and Flowers 1965). Estimates by Robinson (1979) on the relative egg production for *H. americanus* along the eastern coast of Nova Scotia are generally in agreement with our own.

Our study is the first to estimate eggs per recruit for *H. americanus* for different recruit sizes and exploitation rates from three areas in the Canadian Maritimes. The model contains similar assumptions to that of Caddy (1979), which are oversimplifications of reality, such as constant natural mortality rates, stable size-class distribution, constant "knife-edge" recruitment, and growth expressed as molt increment and molt frequency. However, by measuring growth by molt increments and frequency, the parameters used are probably accurate within the size range of the majority of lobsters caught commercially and within the size range for lobster management purposes. The egg-per-recruit model is most sensitive to changes in size at maturity and less sensitive to changes in intermolt period and fecundity for similar sizes. At similar fishing mortalities and recruit sizes for the three areas, Northumberland Strait lobsters with the lower sizes at maturity produced more eggs per recruit compared with that of the Bay of Fundy lobsters (Fig. 5A, 5C). Approximations of growth, especially proportion molting, and of the extrusion factor beyond three to four molts of current recruit size are based on limited empirical data. This emphasizes the need for further research into the understanding of growth and reproduction in large mature lobsters under field conditions. Although the predicted eggs per recruit will vary quantitatively, depending on the parameter values used, the general trends revealed by these analyses (Fig. 5) should remain similar for other parameter values.

Management Implications

Most recruited lobsters in the Canadian Maritimes are subject to high fishing mortality prior to egg extrusion (Paloheimo 1963; Robinson 1979; Campbell 1980). Consequently, the lobster fishery is supported principally by newly recruited lobsters. In many areas of the Canadian Maritimes, 70–95% of the lobsters removed each year are in the first molt into legal size (Robinson 1979; Campbell 1980). With recruit sizes that are close to or below the onset of maturity, the small or less fecund segment of the female population is important in contributing to annual egg production. The first 30–40 mm CL after recruit size of the female population contributes to at least two-thirds of total egg production in an area (Fig. 4).

The lobster resource in central Northumberland Strait and the eastern coast of Nova Scotia appears to be overfished in terms of its reproductive potential. During the past 80 yr, lobster landings have fluctuated but generally declined in both central Northumberland Strait and the eastern coast of Nova Scotia so that, by 1980, landings were below 10% of early 1900 catches (Robinson 1979; Campbell and Mohn 1983). Robinson (1979) suggested that "recruitment overfishing" was the prime cause of the decline in lobster landings in both areas. For eastern Nova Scotia a number of additional hypotheses have been put forward (see Dadswell 1979; Wharton and Mann 1981; Pringle et al. 1982; Harding et al. 1983).

There are fewer eggs per recruit at current fishing mortalities for the Bay of Fundy area (Fig. 5A) than for either of the other two areas (Fig. 5B, 5C). Despite the lower egg production, the Bay of Fundy area has maintained relatively productive and stable landings for the past 30 yr (Robinson 1979; Campbell and Mohn 1983) whereas declines in landings for the other two areas have occurred. This apparent contradiction may be due to a large continental shelf area of the Gulf of Maine providing sufficient refugia to protect reproductive lobsters from high exploitation (Anthony and Caddy 1980; Stasko 1980a, 1980b). With low survival to maturity of the inshore lobster populations, the mature lobsters moving to and accumulating in the offshore areas (Stasko and Campbell 1980) may constitute a "refugium" in space that produces larvae contributing to recruitment in the inshore fishery (Stasko 1978). Offshore mature lobsters may also move into shallow inshore grounds during summer months and into deeper water in winter months (Cooper and Uzmann 1980). Similar to the Gulf of St. Lawrence, the closed fishing season in the Bay of Fundy during the summer months may also constitute a refugium in time (Anthony and Caddy 1980). However, with increased exploitation of mature lobsters such as near Grand Manan in recent years (Campbell and Duggan 1980), recruitment overfishing in the Fundy area may result.

In contrast, the fact that the eastern Nova Scotia lobster production area constitutes a narrow band along the entire nearshore Atlantic coastline of Nova Scotia reduces the likelihood of sufficient refugia for reproducing females to withstand high fishing pressure and biotic and/or abiotic perturbations. Limited evidence indicates that lobsters move short distances in this area (Wilder 1974). Other factors may also be operating to keep lobster densities down in eastern Nova Scotia (Robinson 1979; Harding et al. 1983). In spite of higher egg production per recruit in eastern Nova Scotia than in the Bay of Fundy and Northumberland Strait (at equivalent fishing mortalities and current recruit sizes), stocks have declined. An even higher egg production per recruit may be necessary for eastern Nova Scotia to prevent recruitment overharvesting.

Little is known about stock–recruitment relationships for *H. americanus* in the Canadian Maritimes. Attempts to show a relationship between abundance of larval stages and parent stock of *H. americanus* have been unsuccessful (Scarratt 1964, 1973). Despite the uncertainties of stock–recruitment relationships, a proposed management strategy (Pringle et al. 1983) of increasing minimum legal (recruit) sizes by approximately one molt increment for the three areas is supported by the results of this study. Increasing the minimum legal size

would increase the number of eggs per recruit. This would help to avert potential declines of lobsters in the Fundy area and help rebuild collapsed lobster populations in areas such as eastern Nova Scotia and central Northumberland Strait. However, increases in egg production do not necessarily guarantee increased recruits into the fishery 5–8 yr later. Environmental factors such as temperature, substrate type or shelter, food availability, competition, predation, and disease may play an important role in limiting *H. americanus* larval and juvenile numbers in an area (Wilder 1965). Clearly, further research is required to determine the sources and levels of recruitment for lobsters in the Canadian Maritimes.

Acknowledgments

We thank G. A. P. Black, D. R. Duggan, M. D. Eagles, D. E. Graham, S. Hamet, D. R. Maynard, and A. M. Williamson for technical assistance, F. Cunningham for drawing the figures, and D. E. Aiken, R. W. Elner, G. P. Ennis, R. K. Mohn, J. D. Pringle, and M. Sinclair for helpful comments on earlier drafts of this paper.

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Mysid Life History and Seasonal Variation in Predation Pressure on Zooplankton

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MURTAUGH, P. A. 1983. Mysid life history and seasonal variation in predation pressure on zooplankton. Can. J. Fish. Aquat. Sci. 40: 1968–1974.

The bivoltine life history of *Neomysis mercedis* in Lake Washington, Seattle, results in seasonal variation in population size structure that influences the amount and quality of predation suffered by its zooplankton prey. Population densities and size–frequency data for *Neomysis* are combined with information on the influence of body size on feeding rate and composition of the diet to predict relative predation intensity on five size classes of *Daphnia* over a 27-mo period. An imperfect relationship between mysid numbers and expected predation intensity and seasonal fluctuations in the relative vulnerability of different-sized prey are two consequences of the mysid's pattern of life history.

MURTAUGH, P. A. 1983. Mysid life history and seasonal variation in predation pressure on zooplankton. Can. J. Fish. Aquat. Sci. 40: 1968–1974.

Une conséquence du cycle de vie bivoltin de *Neomysis mercedis* dans le lac Washington, à Seattle, est une variation saisonnière de la structure par taille de la population, qui influe sur la quantité et la qualité de la prédation à laquelle sont soumises les proies zooplanctoniques de cet organisme. Nous avons combiné les données sur les densités de population et la fréquence des tailles de *Neomysis* avec celles touchant l'influence de la grosseur du corps sur le taux d'alimentation et la composition du régime alimentaire afin de prédire, sur une période de 27 mois l'intensité de prédation relative sur cinq classes de grosseur de *Daphnia*. Comme conséquence du cycle de vie des mysides, on observe une relation imparfaite entre le nombre de ces derniers et l'intensité de prédation anticipée, d'une part, et les fluctuations saisonnières de vulnérabilité relative de proies de différentes grosseurs, d'autre part.

Received February 1, 1983
Accepted July 25, 1983

Reçu le 1 février 1983
Accepté le 25 juillet 1983

A common exercise in studies of predators thought to be important in affecting zooplankton community structure is the estimation of the fraction of prey biomass consumed per unit time. These calculations have been done for many animals, including planktivorous fishes (e.g. Lane 1979), copepods (Brandl and Fernando 1979), and *Chaoborus* larvae (review by Pastorok 1980). Usually, a single feeding rate representative of the most important predatory stage of the animal is combined with abundance data to arrive at an aggregate feeding rate for the predator population; the influence of predator age on the selectivity and rate of feeding has rarely been studied (but see Thompson 1975). Accurate models of predator–prey interactions require more detailed information on age-specific feeding behavior of the predator, as well as on temporal variation in the age structure of the predator population (Hassell 1978).

Freshwater mysids are effective predators on zooplankton (Cooper and Goldman 1980; Lasenby and Fürst 1981), and there is some evidence that mysids can influence zooplankton species composition (Richards et al. 1975; Rieman and Falter 1981; Kinsten and Olsén 1981; Murtaugh 1981a). Populations of *Mysis relicta* in lakes show pulsed reproduction and generation times of 1–4 yr (data reviewed by Morgan 1980), so there may be pronounced temporal fluctuations in size structure influencing the quantity and quality of predation suffered by the zooplankton.

In this paper, I examine the ways that the life history of the mysid *Neomysis mercedis* causes seasonal variation in predation pressure on zooplankton. In Lake Washington, Seattle, young *Neomysis* are released from the brood pouch when they are about 3 mm long, and they grow through a series of molts to sizes as large as 17 mm. Since there are two generations per year, the population is alternately dominated by large and small individuals. I present information on the influences of body size on feeding rate and composition of the diet and

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Printed in Canada (J7224)
Imprimé au Canada (J7224)

develop refined predictions of the total predation pressure due to *Neomysis* incorporating effects of the size structure of the population.

Methods

Assessing Mysid Density

Specimens of *Neomysis mercedis* were collected in daytime sampling at a 20-m-deep station in Lake Washington, Seattle, every 2 or 3 wk for 27 mo in 1978–80. A small epibenthic dredge was towed in short hauls along the lake bottom; mysids were either preserved immediately in 10% Formalin or transported live to the laboratory in jars of surface water. For each sampling date usually 50–100 (range 35–461) preserved mysids were measured under a dissecting microscope. Mysid size was recorded as dorsal carapace length, from the apex of the rostrum to the posterior-most extension of the carapace along the dorsal midline. Total body length Y (millimetres from apex of rostrum to apices of telson) can be estimated from the carapace length X (millimetres) according to the regression equation $Y = 0.816 + 3.093X$ ($N = 109$, $r = 0.99$).

Two epibenthic dredges were used in the study, each consisting of a D-shaped frame mounted on a small sled. One dredge, used over the entire 27-mo sampling period, was equipped with a 900-μm-mesh net; a second dredge, with a 500-μm-mesh net, was used in the last 8 mo of sampling to gauge the efficiency of the coarse-mesh net in catching small mysids. Data from the second dredge were corrected for the different numbers and sizes of mysids caught so that results from the two sampling devices could be expressed on a uniform basis (Murtaugh 1981c).

Mysid abundance is expressed here as the "local density" of animals in the epibenthic stratum traversed by the dredge, i.e. the number of mysids in a haul divided by the volume of water filtered, with the latter calculated as the product of dredge mouth area and distance traveled (Murtaugh 1981c). Distances were inferred from haul durations and boat speed, assessed in timed traverses of a measured length of lakefront. Since the mysids are benthic by day, bottom sampling should efficiently census the mysid population. Converting local densities near the bottom into estimates of whole-water-column mysid abundance on a per cubic metre or square metre basis has proven difficult, so that here I present exclusively local density data.

Feeding Experiments

In an attempt to quantify the relationship between *Neomysis* size and feeding rate on *Daphnia*, I pooled data from 14 experiments done under various conditions (Table 1). Methods were as described in Murtaugh (1981a): glass jars of filtered lake water and individually pipetted *Daphnia* were provided with one mysid each and placed in complete darkness. Controls lacking mysids were also run to check on natural prey mortality. The contents of the jars were poured through a fine-mesh screen at the end of the trials, and feeding rates were deduced from the number of prey remaining. Results are expressed as clearance rates k (litres per mysid per day) (Gauld 1951):

TABLE 1. Range of conditions in feeding experiments used to obtain the relationship between mysid size and feeding rate. Prey species were *Daphnia pulicaria* and *D. thorata*. "Starvation" duration is the time mysids were kept in filtered lake water before experiments; since mysids reingest fecal material, most animals, including those held 16 d, had material in their guts at the beginning of the experiments and were therefore not truly starved.

Factor	Range of values
Container size	0.10–0.85 L
Initial prey density	22–224 org·L^{-1}
"Starvation" duration	0–384 h
Experiment duration	0.8–6.6 h
Average *Daphnia* size	0.82–2.21 mm

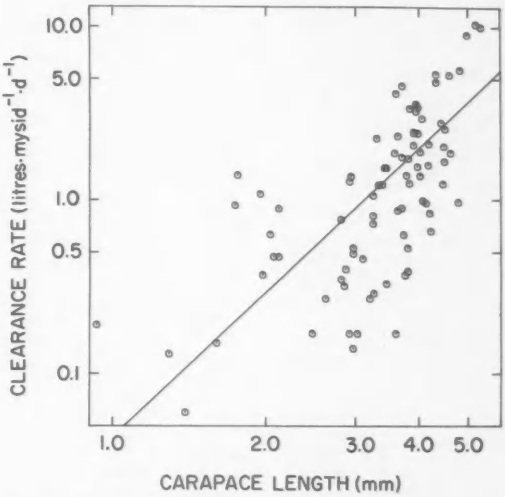

FIG. 1. Relationship between clearance rate on *Daphnia* and mysid size for experiments in small (<0.85 L) containers; log–log plot with nonparametric regression line.

$$(1) \quad k = (v/t)(\ln C_0 - \ln C_t)$$

where C_0 and C_t are the prey concentrations initially and at time t and v is the volume of water available per mysid.

Results and Discussion

Influences of Mysid Size on Feeding Behavior

The size of a predator is one of the most obvious attributes affecting its feeding behavior. For *Neomysis* feeding on *Daphnia*, clearance rate increases dramatically with mysid body size (Fig. 1). There is a great deal of scatter in the data, but nonparametric regression (Mood's method: Tate and Clelland 1957) for the log–log plot yields the relationship $Y = 0.043X^{2.76}$, where Y is the clearance rate on *Daphnia*

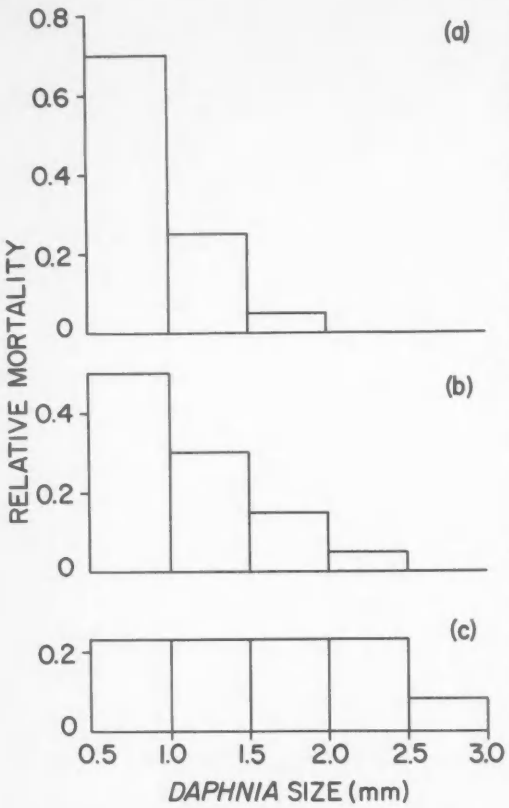

FIG. 2. Idealized representation of size-specific electivities on *Daphnia* for three size groups of *Neomysis*, based on data in Murtaugh (1981b): (a) 0.7- to 2.0-mm carapace (3.0–7.0 mm total body length), (b) 2.0- to 3.0-mm carapace (7.0–10.1 mm total), and (c) 3.0- to 5.3-mm carapace (10.1–17.2 mm total). Ordinate is *W* of Vanderploeg and Scavia (1979), an electivity index proportional to prey mortality.

(litres per mysid per day) and X is mysid carapace length (millimetres).

Some of the variance around the regression line is undoubtedly due to the wide range of conditions in the experiments from which these data were drawn (Table 1). Cooper and Goldman (1982) found that clearance rates of *Mysis relicta* on copepod prey were affected by container size, prey density, and experiment duration. I analyzed the variance in the relationship between clearance rate and body size for *Neomysis* by calculating residuals from the nonparametric regression line shown in Fig. 1 and using these as values of the independent variable in a stepwise multiple linear regression with some of the factors varying among experiments. Even though clearance rates on *Daphnia* in 3.5-L jars were almost three times higher than those predicted from the above regression of feeding rate on body size for trials in much smaller containers (Murtaugh 1981c), the multiple regression on the residuals yielded no significant relationship of clearance rate with container size ($P > 0.4$), probably because of the small range of volumes used (see Table 1). Surprisingly, there was no effect of starvation duration either ($P > 0.2$). This analysis did show that clearance rate tends to decrease with increasing experiment duration ($P < 0.001$) and mean prey size ($P < 0.02$), but attempts to factor out variation due to these sources never resulted in regression lines substantially different from that shown in Fig. 1.

There are reasons that the exponential model forced on the data in these analyses might not be completely appropriate: large mysids might be relatively more impaired by confinement in small vessels than small mysids, and there could be ontogenetic, qualitative changes in mysid feeding behavior with size. The regression line in Fig. 1 does not provide a particularly satisfying fit to the data, especially in the extent to which it underestimates feeding by the largest animals, but it does allow an objective description of the relationship between clearance rate and mysid size.

Predator size may influence qualitative as well as quantitative aspects of feeding behavior. Young stages of many predatory invertebrates are primarily herbivorous (e.g. see Dodson 1975; Gophen 1977), and it has been reported for *Neomysis mercedis* that carnivory is increasingly important in larger individuals (Siegfried and Kopache 1980). I lack quantitative data on the importance of algae in the diet of *Neomysis* in Lake Washington but did find animal remains in the guts of even very small mysids (Murtaugh 1981a). There was heterogeneity in the frequencies of different prey types in the diets of different-sized individuals, but *Daphnia* was an important food for predators of all sizes (Murtaugh 1981a).

The sizes of *Daphnia* consumed by *Neomysis* are definitely dependent on predator size; electivity curves for mysids feeding on *Daphnia* in both the laboratory and the field are given in Murtaugh (1981b). Because these curves were calculated for various prey size intervals and arbitrary size groups of mysids, and because the shapes of the curves were variable (e.g. see Fig. 4 in Murtaugh 1981b), it is difficult to combine these data into a generalized picture of size-specific preference. I nevertheless attempt this in Fig. 2, guided by the observations that small mysids show peak electivity for the smallest prey and large mysids can manage all but the largest *Daphnia*. Note that there is no provision in Fig. 2 for electivity curves with maxima at intermediate prey sizes, as were occasionally observed by Murtaugh (1981b).

PREDICTION OF SEASONAL VARIATION IN PREDATION PRESSURE

The information on the influence of predator size on feeding behavior can be combined with mysid population data to predict the seasonal variation in predation pressure on *Daphnia*. My index of relative predation intensity (*PI*) is simply the product of mysid density and feeding rate, summed over the 20 size classes that were discriminated:

$$(2)\quad PI = \sum_{i=1}^{20} X_i k_i$$

where X_i is the local density of size class i of *Neomysis*

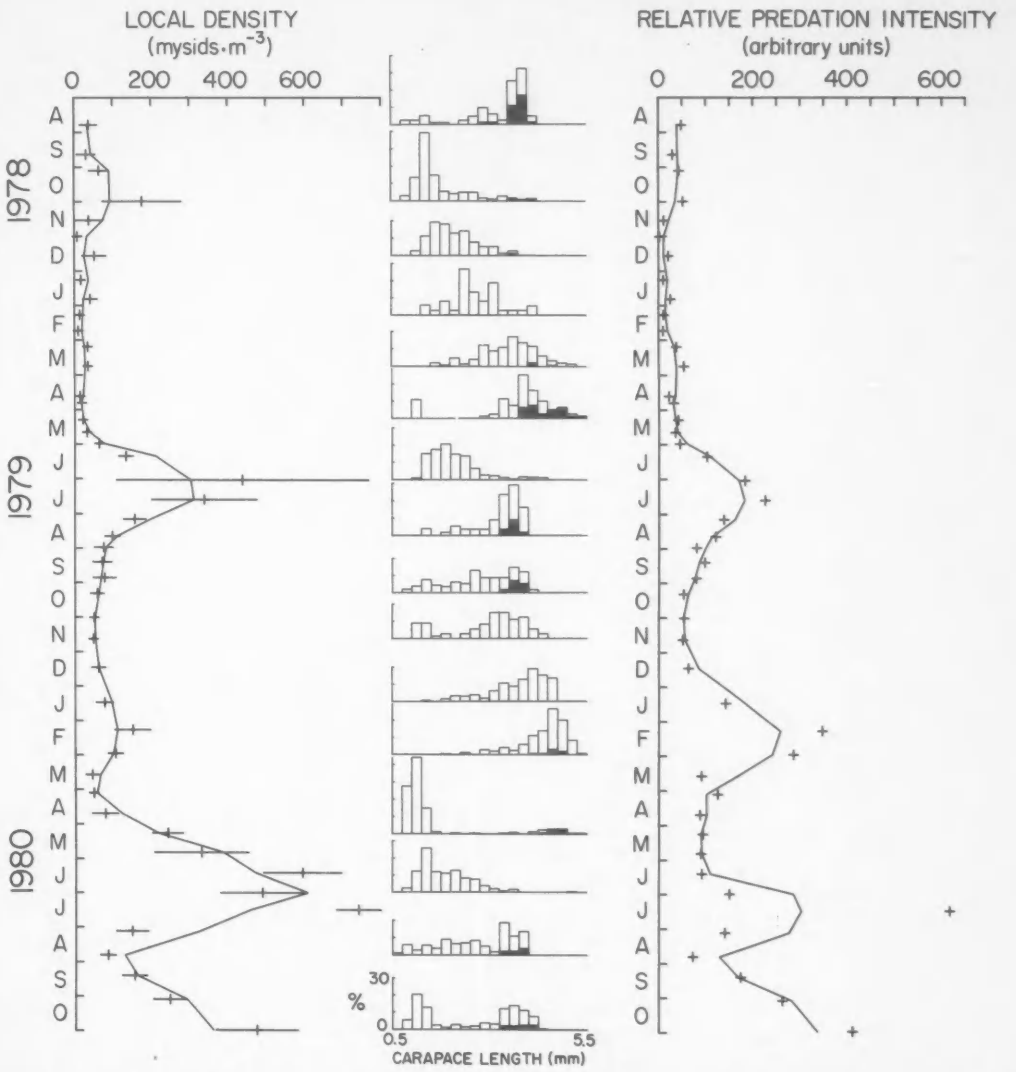

FIG. 3. Estimation of relative predation intensity from field data. Left: average local density (±SE) of daytime bottom hauls, usually 4–10 per date. Line connects three-point running averages. Middle: selected size distributions of *Neomysis* (N = 35–461 measured per date), with base of each histogram aligned with the date it represents. Darkened portions represent gravid females. Right: predicted relative predation intensity, with line connecting three-point running averages.

inferred from dredge hauls (per cubic metre) and k_i is the clearance rate of mysid size class i from the regression line in Fig. 1 (litres per mysid per day). This index represents an aggregate clearance rate for the mysid population in units of reciprocal time, but the scale is purposely arbitrary, since the densities are not expressed on a lakewide basis and the feeding rates likely underestimate in situ values.

This total predation intensity can be apportioned among five *Daphnia* size classes according to the electivities shown in Fig. 2. The clearance rate of mysids in size class i on *Daphnia* in size class j (litres per mysid per day) is given by

$$(3) \quad F_{ij} = W_{ij}\, k_i$$

where W_{ij} is the electivity of mysid size class i on *Daphnia*

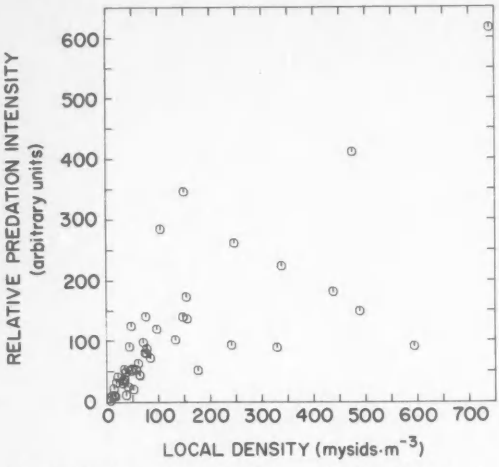

FIG. 4. Relative predation intensity versus local mysid density for 46 dates shown in Fig. 3. There is a significant positive correlation ($r_s = 0.85$, two-tailed $P < 0.001$).

size class j, read from Fig. 2. The amount of the total predation intensity directed at *Daphnia* size class j is then

$$(4) \quad (PI)_j = \sum_{i=1}^{20} X_i W_{ij} k_i.$$

The values of W_{ij} are standardized clearance rates or forage ratios (Chesson 1978; Paloheimo 1979; Vanderploeg and Scavia 1979): in this case, the clearance rate on a particular prey size class divided by the sum of clearance rates over all size classes. Equation 3 therefore implies that k_i is equal to the sum of clearance rates of mysid size class i on the five size classes of *Daphnia*. Actually, the values of k_i were calculated from the overall depletion of different sizes of prey in feeding experiments and would be expected to be smaller than the sums of the *Daphnia*-size-specific clearance rates. But it is probably reasonable to model the aggregate clearance rate (k_i) in the lake, where the pool of available prey is assumed to be very large compared with the numbers that are consumed by mysids, as the sum of the prey-size-specific rates (F_{ij}).

My index of predation intensity is related to the total volume of water cleared of prey by the mysid population per unit time; the actual number of *Daphnia* consumed, of course, depends on the density of prey in the lake and the functional response of the predator. In laboratory work, clearance rate decreased with increasing prey density for *Mysis relicta* feeding on the large copepods *Limnocalanus* (Grossnickle 1978) and *Epischura* (Cooper and Goldman 1982) but was insensitive to changes in prey density for *Mysis relicta* feeding on *Cyclops*, *Diaptomus*, and *Daphnia* (Grossnickle 1978). In perhaps the most revealing work, in situ experiments with *Mysis relicta* in Lake Michigan showed no effect of prey density on clearance rates on cladoceran zooplankton (Bowers and Vanderploeg 1982). The usefulness of my index of relative predation intensity depends on the assumption that clearance rate of *Neomysis* on *Daphnia* is independent of prey density.

My approach to quantifying predation pressure exerted by *Neomysis* ignores several other possible influences on feeding rate, such as temperature (Cooper and Goldman 1982), seasonal variation in the extent or timing of nocturnal vertical migration (Beeton 1960), and long-term adaptation to food availability (Runge 1980). Still, the relative invariance of clearance rates on Cladocera and of selectivities on various prey types reported from the in situ experiments with *Mysis relicta* at several times of the year (Bowers and Vanderploeg 1982) lends hope that environmental modification of the basic pattern of predation modeled here for *Neomysis* is weak enough that my simplified representation produces useful predictions.

Figure 3 shows the results of the calculation of relative predation intensity for the 27-mo sampling period. Note first that the abundance data and size–frequency distributions give a coherent picture of the life history of *Neomysis* in the lake. Releases of young to the water column, as identified by the presence of juveniles and gravid females in the size distributions, are usually accompanied by increases in local density, suggesting that seasonal horizontal movements of mysids do not obscure the basic pattern of life history. *Neomysis* is apparently bivoltine in Lake Washington, with discrete winter and summer generations (Fig. 3), so that the population is alternately dominated by large and small individuals.

The pattern of predation intensity (right panel in Fig. 3) roughly parallels the seasonal variation in mysid abundance, with some discrepancies. A pulse in predation intensity in July 1979 is attributable to an increase in mysid density, but a larger pulse in predation intensity in February 1980 is unaccompanied by a significant increase in mysid numbers. Rather, this increase in predation is accounted for by the gradual maturation of the mysid cohort produced the preceding fall; as the animals grow larger, their per capita feeding rates increase dramatically. A rapid increase in mysid density in April–May 1980 does not result in an immediate increase in predation intensity, because the feeding rates of the just-released juveniles are so low compared with those of the adults they replaced. There is a lag of 1 or 2 mo before the mysids mature enough for their collective feeding activity to show up as a pronounced increase in predation intensity.

Relative predation intensity and local mysid density are strongly correlated ($r_s = 0.85$, two-tailed $P < 0.001$), but there is considerable scatter in the relationship, especially at high mysid densities (Fig. 4). A given density of *Neomysis* can produce either high or low predation intensity, depending on the size structure of the population. Because of the generally inverse relationship between mysid abundance and average body size in the population, mysid density is not necessarily a reliable predictor of total predation intensity.

Figure 5 shows how the predation pressure exerted by *Neomysis* is apportioned among different-sized *Daphnia*. Note that predation is always highest on the smallest *Daphnia*; this is a consequence of the way I chose to summarize the information on size selection by *Neomysis* (Fig. 2). Predation on the largest *Daphnia* is correspondingly low, dropping almost to zero when large mysids are rare in the lake. The effects of size structure of the mysid population are evident in the relative magnitudes of pressure on the different prey size classes at different times of the year. The ratio of the vulner-

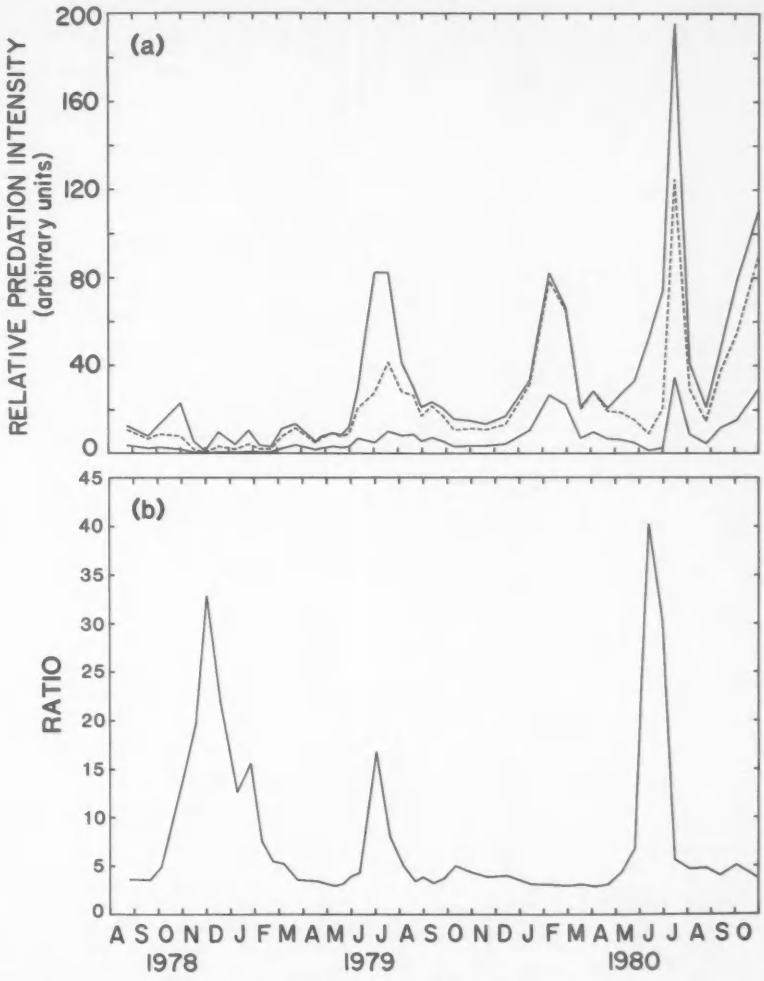

FIG. 5. Seasonal change in relative predation intensity on different-sized *Daphnia*. (a) Relative predation intensity on small (0.5−1.0 mm, upper solid line), medium (1.5−2.0 mm, broken line), and large (2.5−3.0 mm, lower solid line) *Daphnia*. Lines connect actual points for individual dates (no running averages); total predation intensity, summed over five *Daphnia* size classes, is not shown here. (b) Ratio of predation intensity on smallest (0.5−1.0 mm) *Daphnia* to that on largest (2.5−3.0 mm) *Daphnia*.

ability of the smallest *Daphnia* to that of the largest, for example, shows seasonal peaks corresponding to domination of the mysid size distribution by juveniles incapable of eating the largest prey (Fig. 5b). A seasonal succession of *Daphnia* species has been observed in recent years in Lake Washington (Edmondson and Litt 1982), and it is tempting to postulate a relationship to these seasonal shifts in the quality of mysid predation. A preliminary comparison of the mysid data with the timing and nature of the *Daphnia* species replacements, however, fails to support this hypothesis (P. A. Murtaugh, unpublished data).

The temporal variation in the relative vulnerability of different-sized zooplankton to predation by *Neomysis* implies that prey populations will be subject to seasonally dynamic and perhaps unpredictable selective pressures. Invertebrate predators, which usually feed disproportionately on small prey, have been considered an important force in the evolution of cladoceran life histories (Lynch 1980), but for zooplankton coexisting with freshwater mysids, the optimal life history may be an elusive, transitory phenomenon.

Clearly, for a predator such as *Neomysis*, with strong seasonal variation in age structure and a strong dependence of feeding behavior on body size, the size structure of the predator population should be considered in any attempt to estimate predation intensity. Total predator abundance may not be a very revealing indicator of either the quantity or quality of predation actually occurring in the lake.

Acknowledgments

I thank W. T. Edmondson, B. W. Frost, D. A. Soluk, H. A. Vanderploeg, H. Welch, and T. M. Zaret for reading earlier versions of this manuscript, and A. H. Litt for logistic support. This work was funded by National Science Foundation grants DEB 77-12966 and DEB 80-0906 to W. T. Edmondson and by a grant from the Office of Water Research and Technology (Project No. A-096-WASH), U.S. Department of the Interior. The manuscript was prepared during a postdoctoral fellowship at the University of Alberta supported by the Alberta Environmental Research Trust.

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Sea Urchin (*Strongylocentrotus droebachiensis*) Aggregating Behavior Investigated by a Subtidal Multifactorial Experiment

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We performed a multilevel factorial field experiment to identify the effects of five factors on sea urchins' (*Strongylocentrotus droebachiensis*) aggregating behavior. The factors were (1) source of urchins (kelpbed or barrens), (2) density of urchins (high or low), (3) location of treatment (kelpbed or barrens), (4) the presence and type of invertebrate predators (crabs or lobsters), and (5) season (summer or winter). These manipulative experiments were performed in flexible, resilient cages designed to withstand the severe wave surge in Nova Scotia's shallow subtidal environment. Interactions identified by ANOVA among the various factors showed that urchins aggregate more at high ($20 \cdot m^{-2}$) than at low ($4 \cdot m^{-2}$) density. The presence of lobsters in the kelpbed, and of crabs in the barrens, triggered the formation of even larger aggregations. These aggregations remain in the open even in the presence of predators. We argue that this behavioral mechanism (a defensive aggregation response to lobsters in the kelpbed) is the trigger that precipitates widespread destructive urchin grazing and the transformation of kelpbeds to barrens. Lobsters thus play two opposite roles. At low urchin density lobsters keep urchins in hiding and thereby contribute to kelpbed persistence. At higher urchin density, lobsters trigger the formation of large, exposed urchin aggregations that graze destructively on kelp. Urchin responses to predators are probably mediated by a combination of conditioning and sensitivity to biochemical cues. The large-scale change in community structure, from kelpbed to barrens, can thus be understood in terms of the adaptive behavioral responses of individual organisms. We review the roles of other predators in this system and show that they have varying effects on the intensity of urchin grazing, depending on urchin density, season, and habitat type.

BERNSTEIN, B. B., S. C. SCHROETER, AND K. H. MANN. 1983. Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behavior investigated by a subtidal multifactorial experiment. Can. J. Fish. Aquat. Sci. 40: 1975–1986.

Nous avons mené sur le terrain une expérience multifactorielle en vue d'identifier les effets de cinq facteurs sur le comportement d'association de l'oursin de mer commun (*Strongylocentrotus droebachiensis*). Les facteurs étudiés ont été (1) la source des oursins (lit de varechs ou fond dénudé), (2) la densité des oursins (élevée ou faible), (3) l'endroit du traitement (lit de varech ou fond dénudé), (4) la présence et le type de prédateurs invertébrés (crabes ou homards) et (5) la saison (été ou hiver). Ces manipulations ont été effectuées dans des cages résilientes flexibles, conçues pour résister au déferlement des lames dans l'environnement subtidal peu profond de la Nouvelle-Écosse. Les interactions identifiées par ANOVA entre les divers facteurs démontrent que les oursins se rassemblent davantage à une densité élevée ($20 \cdot m^{-2}$) qu'à une densité faible ($4 \cdot m^{-2}$). Les associations sont encore plus fortes en présence de homards sur les lits de varechs et de crabes sur les fonds dénudés. Ces associations demeurent à découvert même en présence de prédateurs. Nous arguons que ce mécanisme éthologique (réponse défensive d'association en présence de homards sur le lit de

Printed in Canada (J7284)
Imprimé au Canada (J7284)

varechs) est le facteur qui déclenche le broutage destructeur chez les oursins et la transformation des lits de varechs en fonds dénudés. Les homards jouent donc deux rôles opposés. À une faible densité d'oursins, ils forcent ces derniers à se cacher, contribuant ainsi au maintien des lits de varechs. À une densité plus élevée d'oursins, les homards déclenchent la formation d'importantes associations d'oursins exposés qui broutent les varechs jusqu'à les détruire. Les oursins réagissent en présence de prédateurs probablement par l'intermédiaire d'une combinaison de conditionnement et de sensibilité à des indices biochimiques. De grands changements de structure de la communauté, soit d'un lit de varechs à un fond dénudé, peut donc s'expliquer en terme de réaction éthologique adaptive d'organismes individuels. Nous examinons le rôle des autres prédateurs dans ce système et démontrons qu'ils produisent des effets variés sur l'intensité du broutage par les oursins, selon la densité de ces derniers, la saison et le type d'habitat.

Received March 7, 1983
Accepted July 27, 1983

Reçu le 7 mars 1983
Accepté le 27 juillet 1983

MUCH evidence points to the large-scale disappearance of algal beds from coastal Nova Scotia, Canada, and their replacement by sea urchin dominated barren grounds between about 1960 and 1980 (Breen and Mann 1976; Mann 1977; Wharton and Mann 1981). Field observations have established that urchins, feeding in dense aggregations, are the proximate cause of the shift from kelpbeds to barrens. The formation of these aggregations, which represents a change in urchin foraging behavior, is thus the trigger point that precipitates the radical change in system state. We have shown (Bernstein et al. 1981) that urchin (*Strongylocentrotus droebachiensis*) aggregating behavior is flexible. Urchins, even at relatively high densities, hide during the summer when large predatory fish are present and forage only at night when the fish are inactive. The presence of crabs caused urchins in the laboratory to aggregate in the open as a defensive clumping response. This led us to hypothesize that a defensive clumping response to invertebrate predators in the kelpbed (crabs or lobsters) could trigger the formation of destructive grazing aggregations, once urchin density had passed a critical threshold.

This is intriguing because it implies that predation, even in this relatively simple system, can be either stabilizing or destabilizing, depending on the type of predator and urchin density. In addition, a behavioral rather than a numerical change in the response of a mobile and behaviorally flexible prey to a single predator may provoke a large-scale shift in ecosystem state. This provides the possibility for understanding in detail the mechanisms that link the behavior of individual organisms to large-scale features of community structure. The field experiments we describe below were undertaken in an attempt to identify the operation of the behavioral trigger point in aggregation formation. We wished to test the hypothesis that aggregating behavior is intensified by defensive responses to certain predators. In addition, we wanted to determine the ways in which major environmental features such as season and habitat (kelpbed or barren) interacted to set limits to urchins' aggregating behavior.

Study Site

We performed the experiments at 8 to 10 m of depth at Green Island, near Cape Sable on the exposed southwest coast of Nova Scotia. This site included healthy *Laminaria* beds and established barrens in close proximity, as well as populations of urchins at densities characteristic of these two habitats. In the kelp area, the substrate consisted of large granite boulders, the largest being several metres in diameter. Algal cover approached 90% and consisted primarily of *Laminaria longicruris* and *L. digitata* with an understory of *Chondrus crispus*. *Desmarestia viridis* was seasonally abundant in the summer. Nova Scotia's nearshore subtidal kelpbeds are described in greater detail in Mann (1972). Urchin densities in the kelp were low ($<5 \cdot m^{-2}$); all individuals were large (>35 mm) and hidden in crevices in both winter and summer. This area was exposed to severe winter storms from the west and northwest. Gales lasting for several days, with wind velocities in excess of 70 $km \cdot h^{-1}$ and swells to 7 m were common during the winter experiments.

The barren area was slightly less exposed. The substrate was granite boulders (to 1 m diameter) with occasional patches of coarse sand. There was scattered *Agarum cribrosum* but no *Laminaria* or *Chondrus*. Urchin densities were higher than in the kelp area ($20-30 \cdot m^{-2}$) and these were predominantly exposed rather than hidden. Water temperatures at both sites ranged from 1°C in the winter to 12°C in the summer.

Materials and Methods

EXPERIMENTAL DESIGN

The field experiments were designed to detect the effects of five factors on sea urchins' aggregating behavior. These factors were (1) source of urchins (kelpbed or barrens), (2) density of urchins (high or low), (3) location of treatment (kelpbed or barrens), (4) the presence and type of invertebrate predators (crabs or lobsters), and (5) season (summer or winter).

Our previous work had indicated the importance of each of these factors in aggregating behavior. Urchins from the barrens are starved relative to kelpbed urchins. This difference in nutritional state affects their movement patterns (Bernstein et al. 1981; Mattison et al. 1977) and most probably their response to biochemical cues. Clumping is more prevalent at high urchin densities (Bernstein et al. 1981). The kelpbed and the barrens differ in the amount and type of food and shelter and harbor distinct suites of predators. Finally, both inver-

TABLE 1. Factorial experimental design. Urchins from kelpbed and barrens were transplanted to cages in the kelpbed and in the barrens, at both high and low densities, and in the presence and absence of predators. All treatments were performed in winter and summer.

Season	Source of urchins	Habitat of experiment	Density of urchins	Predators	Replicates	
					Winter	Summer
				Crabs	3	3
			High	Lobsters	2	3
				None	3	3
		Kelpbed				
				Crabs	2	3
			Low	Lobsters	4	2
				None	3	3
	Kelpbed					
				Crabs	3	4
			High	Lobsters	3	1
				None	3	3
		Barrens				
				Crabs	3	2
			Low	Lobsters	4	3
				None	3	3
Winter + summer						
				Crabs	3	3
			High	Lobsters	3	2
				None	3	3
		Kelpbed				
				Crabs	2	3
			Low	Lobsters	3	2
				None	2	2
	Barrens					
				Crabs	3	3
			High	Lobsters	1	3
				None	2	3
		Barrens				
				Crabs	3	3
			Low	Lobsters	2	2
				None	3	3

tebrate predators and season of the year affect urchins' clumping and foraging behaviors. We designed the treatments as a five-way factorial experiment with replication (Table 1). We collected large sea urchins from kelpbed and barrens habitats and transplanted them to cages in the kelpbed and in the barrens, at high or low urchin densities, and in the presence and absence of invertebrate predators.

We utilized the factorial design because of its power and efficiency (Snedecor and Cochran 1967; Underwood 1981) and because we were specifically interested in interactions among the factors. All factors were fixed effects, and the experiment was thus a model I analysis of variance (ANOVA), with all significance tests performed with the replicate or residual error in the denominator of the F-test. The level of replication was determined in part by logistical constraints. We did, however, perform pilot experiments that demonstrated that three replicates provided sufficient power to detect the predicted changes in clumping behavior.

Successful manipulations required the design of cages that could withstand the severe environmental conditions without interfering with urchin behavior. This task was complicated by the hardness of the granite substrate, which made drilling holes for cage supports unfeasible, and the extremely cold water temperatures, which prevented the use of marine epoxies. We developed flexible, circular cages made of 5.6-cm monofilament mesh stretched over plastic hoops and anchored by guy ropes to a grid of chains (Fig. 1). This design was very transparent to wave surge and was quite resilient so long as the guy ropes were regularly inspected and maintained. All the cages survived several 3-d gales, and half of them survived an 8-d storm.

We deployed 36 cages, 18 in each habitat. All were 1.2 m in diameter, covering an area of 1.0 m^2. This was large enough to ensure a variety of cryptic and exposed habitats in each cage. We avoided placing the cages on open sand patches or the flat faces of huge boulders and placed them in habitats with the same mix of substrates. The cage walls acted as additional structure, and urchins responded to them as they did to natural ledges and crevices (see Discussion for an analysis of possible cage effects). Urchin escape rates were extremely low (<10%), but about one third of the lobsters and crabs escaped in the summer when these crustaceans were most active; all such experiments were discounted and repeated immediately.

Each replicate treatment ran for 3–6 d, depending on the weather. Low- and high-density treatments contained 4 and 20 urchins, respectively. This low density ($4 \cdot m^{-2}$) is near the upper range of urchin densities in healthy, persistent

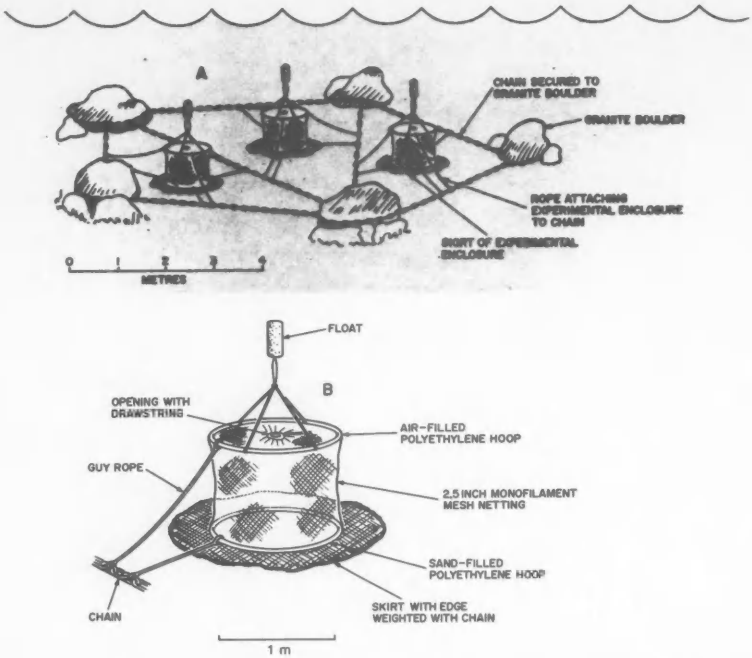

FIG. 1. (A) Cage system. Guy ropes were fastened to a grid of chains anchored to large boulders. Small buoys kept the cages erect, but allowed them to flex in response to surge. Each cage was 1.2 m in diameter and 1 m high. (B) Details of an individual cage.

Laminaria beds. The high density ($20 \cdot m^{-2}$) is below that at which urchins are found in exposed feeding fronts ($80 \cdot m^{-2}$) (Bernstein et al. 1981). We selected $20 \cdot m^{-2}$ because we wished to observe urchin behavior at the threshold of clump formation. Field observations of urchin grazing in St. Margaret's Bay and pilot experiments suggested that this occurred at about $20-30$ urchins $\cdot m^{-2}$. Predator treatments contained one lobster or two crabs, with their claws banded. All animals were used for one replicate only and were then discarded. Urchins and crabs were captured locally; lobsters were either captured locally or purchased from fishermen immediately after capture.

Data were collected by scuba divers who inspected each cage and recorded their observations by mapping the location of each urchin and predator. They noted whether each urchin was hidden or exposed (as in Bernstein et al. 1981) and the size and location of all clumps of two or more urchins. Replicates were discarded if more than 25% of the urchins could not be located or if the predators had escaped.

ANALYSIS

We calculated the following variables for each replicate treatment: mean clump size, percent of urchins clumped, and percent of urchins in contact with the cage wall. These were calculated separately for all urchins in the cage, urchins in the open, and urchins in hiding. In addition, we calculated the percent of urchins in each cage in hiding.

As in Bernstein et al. (1981), we defined a clump as any group of two or more urchins in contact. We calculated mean clump size by dividing the total number of urchins by the number of separate urchins or groups of urchins in the cage. Thus, a cage in which four urchins were distributed as a group of two and two separate individuals would have mean clump size or 4/3 or 1.33. Clump sizes of 0 occurred occasionally. If all the urchins in a cage were in hiding, for example, then the mean clump size of urchins in the open was defined as 0. Clump size in hiding was calculated on the same basis as urchins in the example above.

We analyzed each variable separately with ANOVA (fixed effects, general linear model, unbalanced design). We chose to analyze each variable for the total population of urchins and again for those portions of the population in open and cryptic subhabitats. We did this, despite the slight redundancy, because our previous work (Bernstein et al. 1981) showed that urchins in these subhabitats sometimes behave differently. This approach also enabled us to determine which component of the urchin population was contributing most of the overall response.

Percentage values were transformed prior to analysis with the arc sine square root transformation. Mean clump size values were transformed to $\log_{10}(x + 1)$ to counter effects of

TABLE 2. Means of the replicates of each experimental treatment outlined in Table 1. All variables calculated for each treatment are shown. Two or more urchins in contact were considered a clump. "Total" variables were calculated using all urchins in each cage, while "open" and "cryptic" variables were calculated only from urchins in these subhabitats.

Source of urchins	Habitat of experiment	Density of urchins	Predators	% cryptic	Mean clump size			% clumped			% on wall		
					Total	Open	Cryptic	Total	Open	Cryptic	Total	Open	Cryptic
(a) Means for winter experiments													
Kelpbed	Kelpbed	High	Crabs	31.4	2.1	1.9	3.4	69.0	60.7	80.0	47.0	48.3	49.0
			Lobsters	7.7	2.9	1.5	1.5	83.0	85.0	50.0	36.5	34.0	50.0
			None	17.2	1.7	1.6	2.3	69.0	51.0	33.3	42.7	37.0	77.7
		Low	Crabs	50.0	1.5	1.0	0.5	50.0	50.0	0.0	87.5	50.0	37.5
			Lobsters	31.3	1.0	1.0	0.8	0.0	0.0	0.0	91.8	87.0	75.0
			None	33.3	1.1	1.3	0.7	16.7	33.3	0.0	36.0	27.7	33.3
	Barrens	High	Crabs	8.7	2.1	2.1	1.7	64.3	63.3	33.3	28.7	29.7	0.0
			Lobsters	33.9	1.6	1.4	2.1	43.7	34.7	73.3	76.0	81.7	60.0
			None	42.1	1.7	1.4	1.6	58.0	39.3	53.7	55.0	25.3	95.3
		Low	Crabs	80.6	1.1	0.7	1.1	16.7	0.0	16.7	72.3	0.0	89.0
			Lobsters	50.0	1.3	1.3	1.3	31.3	41.5	25.0	81.3	45.8	87.5
			None	30.6	1.3	1.2	0.8	39.0	22.3	22.3	66.7	69.0	33.3
Barrens	Kelpbed	High	Crabs	12.5	1.5	1.5	2.0	47.3	41.7	33.3	26.3	27.0	33.3
			Lobsters	11.7	3.1	3.7	1.3	88.0	90.7	44.7	45.3	40.0	55.7
			None	22.7	2.1	2.2	1.7	71.0	75.0	46.7	27.0	21.3	40.0
		Low	Crabs	33.3	1.0	1.0	0.5	0.0	0.0	0.0	41.5	75.0	25.0
			Lobsters	8.3	1.3	1.7	0.3	25.0	33.3	0.0	77.7	77.7	0.0
			None	12.5	1.3	1.4	0.5	50.0	58.5	0.0	0.0	0.0	0.0
	Barrens	High	Crabs	21.0	2.8	2.4	2.0	72.0	73.7	30.7	35.0	56.0	0.0
			Lobsters	30.9	1.3	1.2	1.6	45.5	41.5	75.0	48.5	53.5	66.5
			None	24.8	1.9	1.9	2.2	59.7	52.3	81.0	63.7	56.0	81.0
		Low	Crabs	27.0	1.2	1.0	1.0	16.7	0.0	33.3	52.3	50.0	33.3
			Lobsters	75.0	1.3	1.0	1.5	50.0	0.0	67.0	75.0	0.0	100.0
			None	32.1	1.2	1.0	1.5	25.0	0.0	50.0	66.0	50.0	50.0
(b) Means for summer experiments													
Kelpbed	Kelpbed	High	Crabs	52.7	2.0	2.1	1.7	75.3	79.3	52.3	53.3	68.7	63.3
			Lobsters	61.0	2.4	2.8	2.6	80.3	83.3	61.3	27.0	41.7	23.7
			None	67.9	1.7	1.7	1.9	56.0	38.7	60.7	63.0	39.0	75.3
		Low	Crabs	73.3	1.2	0.4	1.0	13.3	16.7	0	20.0	16.7	33.3
			Lobsters	37.5	1.0	1.0	1.0	0	0	0	37.5	33.5	25.0
			None	33.3	1.0	1.0	0.7	0	0	0	52.7	77.7	33.3
	Barrens	High	Crabs	64.9	2.4	1.5	2.7	73.2	44.5	71.0	62.2	33.5	67.0
			Lobsters	88.0	2.4	1.0	3.0	82.0	0	93.0	82.0	100.0	87.0
			None	43.1	1.6	1.9	1.4	57.3	68.0	47.7	71.7	66.3	78.3
		Low	Crabs	58.3	1.0	1.0	1.0	0	0	0	87.5	75.0	75.0
			Lobsters	43.3	1.2	1.0	1.0	20.0	0	25.0	91.7	83.3	50.0
			None	22.3	1.3	1.3	0.3	25.0	25.0	0	52.7	41.7	16.7
Barrens	Kelpbed	High	Crabs	28.6	1.5	1.4	1.7	47.3	31.3	21.0	28.3	20.7	56.3
			Lobsters	49.0	2.1	2.2	2.0	71.5	46.5	76.0	64.0	65.5	36.5
			None	28.3	1.8	1.9	1.7	66.7	67.7	55.7	40.3	47.7	33.3
		Low	Crabs	33.3	1.8	1.3	0.4	75.0	58.3	16.7	41.7	25.0	16.7
			Lobsters	87.5	2.7	0.5	2.8	75.0	0	83.5	0	0	0
			None	37.5	1.3	1.2	1.5	50.0	33.5	50.0	62.5	50.0	50.0
	Barrens	High	Crabs	36.3	2.1	2.5	1.8	67.0	69.0	72.7	56.7	31.3	66.7
			Lobsters	44.0	2.0	1.8	2.2	72.0	61.0	86.5	91.5	94.5	86.5
			None	33.8	2.2	1.0	2.5	80.0	0	86.7	70.0	100.0	100.0
		Low	Crabs	47.2	1.0	1.0	1.0	0	0	0	61.0	50.0	66.7
			Lobsters	58.3	1.1	1.0	1.2	16.7	0	22.3	91.7	100.0	83.3
			None	69.4	1.0	0.7	1.0	0	0	0	66.7	66.7	58.3

TABLE 3. *F* values, degrees of freedom (in parentheses), and significance levels for significant main effects and interactions in ANOVA performed on each variable. For simplicity's sake, we have not included a listing of all possible interactions (*$P<0.05$; **$P<0.01$; ***$P<0.001$). Mean square values, if desired, can be reconstructed by multiplying each *F* value by the appropriate error mean square term. Complete ANOVA tables not included because of the large number of variables analyzed.

Source of variation	% cryptic	Mean clump size			% clumped			% on wall		
		Total	Open	Cryptic	Total	Open	Cryptic	Total	Open	Cryptic
Season (winter vs. summer)	10.86(1)**									
Source of urchin (kelpbed vs. barrens)								4.66(1)*		
Habitat of experiment (kelpbed vs. barrens)						4.86(1)*		24.52(1)***	4.60(1)*	9.36(1)**
Density of urchins (high vs. low)		69.31(1)***	46.68(1)***	22.52(1)***	102.53(1)***	67.66(1)***	36.49(1)***			
Season × habitat								6.74(1)*	7.10(1)**	
Source × predators	3.01(2)*									
Season × source × habitat					5.69(1)*					
Season × source × density	4.64(1)*				4.34(1)*				4.26(1)*	
Season × habitat × density		5.74(1)*			11.89(1)***		6.97(1)**	6.68(2)**	6.59(2)**	
Season × habitat × predators										
Source × habitat × density		4.22(1)*			7.05(1)**	6.59(1)*				
Habitat × density × predators		3.51(2)*			4.08(2)*	4.32(2)*				
Season × source × habitat × density					8.40(1)**					
Season × habitat × density × predators								3.16(2)*	5.99(2)**	
Error mean square	530.22697(85)	0.00656(85)	0.01726(85)	1.47479(85)	347.46599(85)	605.23919(85)	1018.66819(85)	434.72656(85)	860.98126(85)	1344.69979(85)

nonnormality. An examination of the variances showed that they did not exceed the limits of robustness of the *F*-test described by Green (1979) and Harris (1975).

We examined significant interactions with interaction plots that displayed the relationships among factors. The 0.05 level was used for all significance tests with the *F*-test.

The interpretation of higher order interactions in a multilevel factorial design can be difficult unless it is based on explicit predictions, or unless it is possible to assign clear biological meaning to them. Fortunately, we have been able to do both (see Results). We gave relatively less attention to effects that, while significant, were smaller or weaker. We found this design, even though complex, invaluable for two reasons. First, our previous studies demonstrated that several factors act together to influence aggregating behavior. The only way to identify how these factors interact in nature is with a factorial experiment. Second, the factorial design provides the most statistically and logistically efficient means of testing for the effects of several factors, either in isolation (main effects) or in combination (interaction effects).

Results

Table 2 presents treatment means for the winter and summer sets of experiments. Table 3 summarizes results of ANOVA by indicating, for each variable, which main effects and interactions were significant. As suggested by Sokal and Rohlf (1969) and Snedecor and Cochran (1967), we discussed in detail only the highest level interactions involving each factor. This is because a simple statement about the effects of one factor is ambiguous when the effect is modified by the action of a second or third factor. For example, it would be inaccurate to say only that clump sizes are larger at high urchin densities, when the size of the effect depends on whether the experiments take place in the kelp or in the barrens and on whether or not a lobster is present. Table 3 displays analyses of variance for these higher level interactions. Table 4 shows means for strongly significant main effects.

CLUMPING

Two variables were measures of clumping behavior: the percentage clumped and the mean clump size. The percentage clumped is somewhat, but not completely, correlated with mean clump size. This is because clump size can increase from 1.0 (when no urchins are clumped) only if the percentage clumped increases. Once some of the urchins are clumped, however, it is possible for mean clump size to increase when those urchins rearrange themselves into fewer, but larger, groups, without changing the percentage clumped. These variables measure slightly different aspects of clumping behavior. Mean clump size is more sensitive to the intensity of aggregation, i.e. the degree to which urchins form large clumps.

The influence of urchin density on both clump size and percentage clumped was conspicuous (Table 4). In general, urchins clump more at high densities, although this effect is modified by the action of other factors. The density effect on clump size is partly a reflection of the higher upper limit on

TABLE 4. Strongly significant main effects. An asterisk indicates that the factor was *not* included in any higher order interactions. The other main effects, particularly density, were strong enough that their influence was apparent even in significant higher order interactions.

Source of variation	% cryptic	Mean clump size			% clumped			% on wall		
		Total	Open	Cryptic	Total	Open	Cryptic	Total	Open	Cryptic
Season										
Winter	29.7									
Summer	43.4									
Source										
Kelp								53.2*	45.7*	
Barrens								45.2	43.0	
Habitat										
Kelp								40.9		37.0*
Barrens								57.8		54.2
Density										
High		1.9	1.8*	2.0*	54.9	49.6	48.7			
Low		1.2	1.0	0.9	19.8	13.7	12.8			
Treatment										
None										
Crabs										
Lobsters										

potential clump sizes in the high-density treatments.

Several significant interactions (Table 3; Figs. 2–4) describe the ways in which the other four factors combine with each other, and with density, to influence clumping behavior. The most important of these is the habitat × density × predators interaction (Fig. 2), which affects both mean clump size and percentage clumped. This demonstrates that at high urchin density, the presence of lobsters increases clumping in the kelpbed, and the presence of crabs increases clumping in the barrens. These predator effects are notable in two respects. First, they are much more marked at high than at low urchin density, unlike most of the other interactions discussed below. Second, the magnitude of the effect of predators on clump sizes is comparable with that of the very strong and pervasive effect of density. The mean clump sizes of 2.2 (high urchin density in the barrens, with crabs) and 2.3 (high urchin density in the kelp, with lobsters) are the largest encountered in any of the statistically significant interactions. Whereas seasonal effects were not statistically significant, mean clump sizes in the high urchin density lobster treatments in the kelp during the winter were higher yet (i.e. 2.9) (Table 2a).

These differences in clump size may seem small (e.g. 1.8 to 2.3 or 2.9), but they represent an important change in the dispersion patterns of urchins in the cages. Clump sizes of around 1.8 typically result from three or four clumps of three or four urchins each in a cage with 20 urchins. Clump sizes much above 2.0, however, always include one clump of at least 8–10 urchins (Table 5). This change in clumping pattern is significant because a clump of 10 grazing urchins is large enough to hold down and cause severe damage to *Laminaria* plants, while a clump of three or four urchins is much less able to do so. In the spring of 1978, we observed the formation of a localized urchin feeding aggregation along the edge of a kelpbed in St. Margaret's Bay (Bernstein et al. 1981). As urchin density increased above $20 \cdot m^{-2}$, groups of two to four urchins appeared, clustered around *Laminaria* holdfasts and stipes. There were occasional clumps of 10 or more urchins holding down entire *Laminaria* plants. As urchin density continued to increase, these large clumps became more frequent and gradually merged to form a solid mass as urchin density approached $100 \cdot m^{-2}$.

We believe these high-density treatments in the kelp with lobsters demonstrate the initial formation of destructive feeding aggregations. The formation of these aggregations depends on high urchin density, the presence of kelp, and the presence of lobsters and represents a defence mechanism against predation. This mechanism explains how small clearings begin appearing in otherwise healthy-looking *Laminaria* beds. Depending on the relative densities of urchins and lobsters, these clearings would then either disappear and reappear in a shifting mosaic or persist and enlarge as more and more urchins aggregated. This latter scenario fits the observed progression of kelpbed destruction in St. Margaret's Bay, Nova Scotia. In that instance, clearings associated with urchin grazing persisted and enlarged until most of the bay had been denuded of kelp (Breen and Mann 1976; K. H. Mann, personal observation). In addition, the fact that urchin clumps were larger in the winter corresponds with observations that destructive feeding aggregations most often form in late fall and winter, probably because large predatory fish are absent during those seasons (Bernstein et al. 1981).

A key feature of destructive feeding aggregations is that they represent a behavior that permits urchins to forage openly, even in the presence of predators (lobsters). Our data show that, in fact, urchins in open subhabitats clump much more in response to lobsters than do those in cryptic subhabitats. For the percentage clumped variable, the habitat × density × predators interaction was statistically significant for urchins in the open, but not for those in hiding (Table 3). For the mean clump size variable, the treatment means (Table 6) indicate that, at high urchin density in the kelp, with lobsters, mean clump size was 2.6 for urchins in the open and only 1.8 for urchins in hiding. Similarly, the percentage clumped was 61% for urchins in the open and only 43% for urchins in hiding.

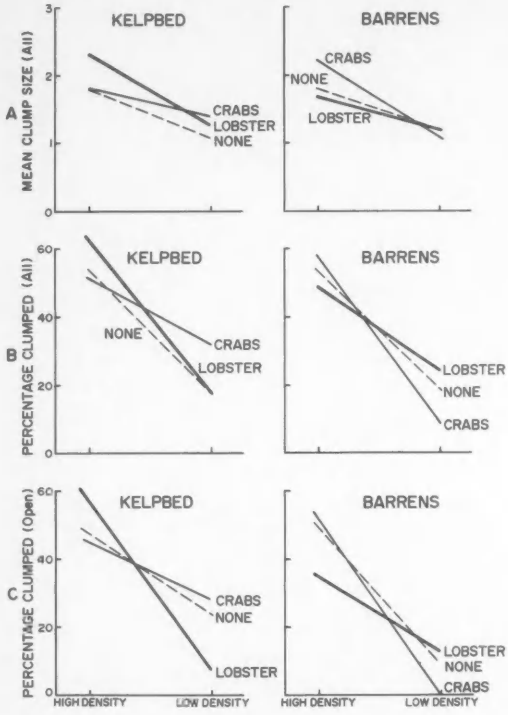

FIG. 2. Interaction plots of the habitat × density × predators interaction for the variables (A) mean clump size for all urchins in the cage, (B) percent clumped for all urchins in the cage, and (C) percent clumped for urchins in the open. This interaction was statistically significant for all three variables (Table 3). Clumping is always greater at high urchin density, and this effect is enhanced in the presence of lobsters in the kelpbed. In contrast, clumping in the barrens at high urchin density is always greatest in the presence of crabs. The degree of clumping thus depends on the particular combination of the three factors. See Tables 5 and 6 for further analysis of the treatment means.

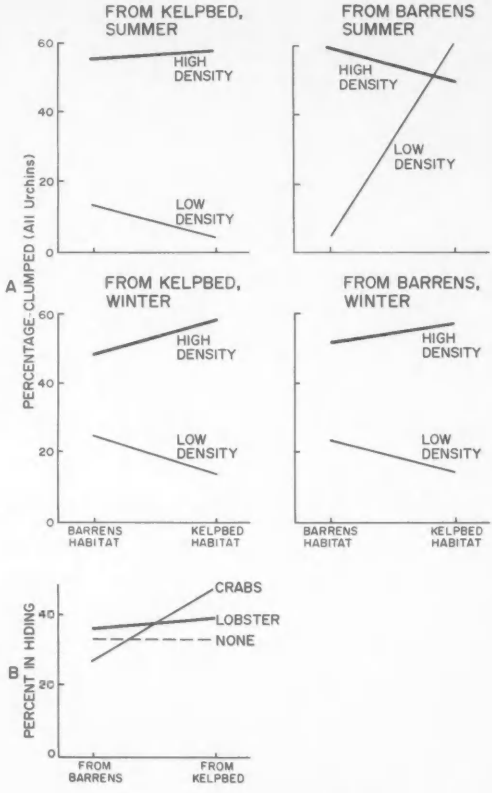

FIG. 3. (A) Interaction plot of the season × source × habitat × density interaction for percent clumped for all urchins in the cage. The pattern of clumping is similar across all conditions, except for the anomalously high clumping of urchins from the barrens at low density in the kelpbed during the summer. (B) Interaction plot of the source × predators interaction for the percent of urchins in hiding. Urchins from the kelpbed hide more in the presence of crabs than do urchins from the barrens. The source of urchins has no effect on clumping in the lobster and control treatments.

We had earlier proposed (Bernstein et al. 1981) that crabs were responsible for inducing urchin clump formation in kelpbeds. We based this suggestion on our observation that crabs induced clumping in the laboratory as a defence mechanism. The present series of experiments demonstrates that urchins will not clump in response to crabs in the kelp, but only in the barrens. Because there was no kelp in the laboratory experiments, these more closely resembled the barren habitat.

Three other significant interactions described additional effects of the factors season, source, habitat, and density on clumping behavior (Table 3). These are season × habitat × density, source × habitat × density, and season × source × habitat × density (Fig. 3A). Since the factors involved in the first two are included in the third, we discuss only this last interaction. It shows (Fig. 3A) that urchins from the barrens clump more in the kelp at low density during the summer than in any other treatment. This is the only instance when the percentage clumped at low urchin density exceeded the percentage clumped at high urchin density. This was not a response to predators, since the urchins were clumped on a *Laminaria* blade. It could have resulted from the increased food supply represented by the *Laminaria* plants in the cages. We have observed that urchins in the barrens will quickly aggregate and feed on drift *Laminaria*. Garnick (1978) and K. H. Mann and B. E. Welsford (Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., unpublished data) have demonstrated that urchins will home on the scent released by another urchin feeding on *Laminaria*. If one of the four urchins in the low-density treatment began feeding first, it is likely the others would have aggregated on it, resulting in a high figure for percentage clumped. At high density, there

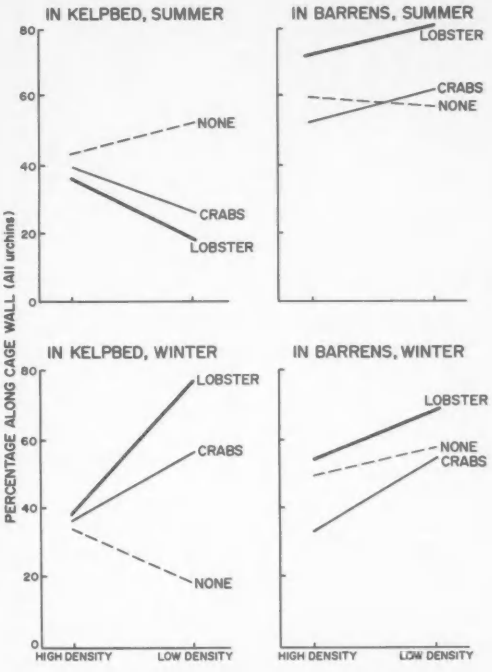

FIG. 4. Interaction plot for the season × habitat × density × predators interaction for the percent along the wall for all urchins in the cage. Except for the summer in the kelpbed, percent along the wall is higher at low than at high urchin density, when predators are present.

would be several urchins feeding on *Laminaria* simultaneously, with several sources of scent. Urchins would thus be dispersed around the cage. Urchins from the kelp did not exhibit this low density aggregation response, presumably because they were well fed.

HIDING

Hiding is an alternative antipredator defence and is complementary to the aggregating behavior described. We found that urchins were more likely to hide in the summer than in the winter (Tables 3 and 4), most probably because large predatory fish are common in the summer but not in the winter, and only very large aggregations are an effective defence against these fish (Bernstein et al. 1981). Season was also involved in a higher level interaction (season × source × density) (Table 3). While significant, the effect was small relative to other interactions, and we therefore do not treat it further.

Urchins from the kelp and barrens also exhibited different hiding behavior. Urchins from the kelp hide more in the presence of crabs than do urchins from the barrens (source × predators) (Table 3; Fig. 3B). This is understandable in view of the fact that urchins in the barrens clump as a defence against crabs, while urchins in the kelp do not. Some aspects of urchins' response to crabs may thus be entrained by the habitat urchins live in and persist even when they are moved to another habitat. There was no analogous hiding response to lobsters.

MOVEMENT

Movement, or fleeing, is a third potential antipredator strategy. Like clumping, it can result from both foraging and antipredator behaviors. Mattison et al. (1977), working with *Strongylocentrotus franciscanus*, showed that urchins in a barren area moved farther than those inside a kelpbed. They interpreted this as foraging behavior in an area with a low concentration of food. The percent of urchins in a cage along the wall reflects the degree of movement in the cage. Urchins fleeing from crabs or lobsters in the cage are more likely to be along the wall. Similarly, urchins attempting to forage along the boundaries of the cage will concentrate along the wall. Figure 4 shows that the percentage along the wall in the crab

TABLE 5. Means and ranges (in parentheses) of the largest urchin clump in each replicate of the treatments in the significant habitat × density × predators interaction. Only at high urchin density in the kelp with lobsters and in the barrens with crabs do clumps larger than 10 occur.

Habitat	Density	Predators	*n*	Total	Open	Cryptic
Kelpbed	High	Crabs	12	5.2(3–8)	3.7(1–6)	3.3(1–6)
		Lobsters	11	7.4(3–13)	6.2(1–13)	3.1(1–10)
		None	12	4.7(2–7)	4.1(1–6)	2.8(1–7)
	Low	Crabs	10	1.7(1–3)	1.8(1–3)	1.3(1–2)
		Lobsters	11	1.5(1–4)	1.2(1–3)	1.5(1–4)
		None	10	1.5(1–2)	1.4(1–2)	1.1(1–2)
Barrens	High	Crabs	13	6.3(3–11)	5.5(2–11)	3.9(1–7)
		Lobsters	9	3.6(2–6)	2.6(1–6)	3.2(2–6)
		None	12	4.8(2–7)	4.3(1–7)	3.2(2–5)
	Low	Crabs	11	1.2(1–2)	1.0(1)	1.2(1–2)
		Lobsters	11	1.5(1–3)	1.1(1–2)	1.5(1–3)
		None	11	1.4(1–3)	1.3(1–3)	1.2(1–2)

TABLE 6. Treatment means averaged across source and season for the habitat × density × predators interaction (Fig. 2). Largest clumps occur in the kelpbed, at high urchin density, in the presence of lobsters, in the open.

Habitat of experiment	Density of urchins	Predators	n	Mean clump size		
				Total	Open	Cryptic
Kelpbed	High	Crabs	12	1.8	1.7	2.2
		Lobsters	11	2.3	2.6	1.8
		None	12	1.8	1.8	1.9
	Low	Crabs	10	1.4	0.7	0.6
		Lobsters	11	1.3	1.0	1.0
		None	10	1.2	1.2	0.8
Barrens	High	Crabs	13	2.2	1.8	2.1
		Lobsters	9	1.7	1.4	2.1
		None	12	1.8	1.8	1.9
	Low	Crabs	11	1.1	0.9	1.0
		Lobsters	11	1.2	1.0	1.2
		None	11	1.2	1.0	0.9

and lobster treatments is generally higher at low than at high urchin densities. Urchins at low density are more likely to attempt to flee, since the clumping defence is not available to them. This, in fact, reflects what happens when urchins are placed into a healthy kelpbed with very low natural urchin densities: they rapidly disperse (Breen and Mann 1976; B. B. Bernstein, personal observation). Table 3 shows that predators do not affect the percentage along the cage wall of urchins in hiding, but only of those in the open. Urchins in hiding are presumably relatively safe from predation and respond only to habitat (Table 3). More of them, however, are found along the wall in the barrens than in the kelp (Table 4). Since this is not a response to predation, it implies that urchins in the barrens forage more widely than do those in the kelp, even when they are in hiding. They are able to remain in hiding because many of the spaces between the boulders are interconnected and act as traps for drift algae.

Discussion

CAGE EFFECTS

The interpretation of our results is contingent on an identification and understanding of any potential biases resulting from the cage treatments. There are three issues to consider: (1) do the cages affect the physical–chemical environment and thus urchin behavior, (2) do the cages affect the physical–chemical environment in the control and predator treatments differently, and (3) is there an interaction between cage effects and urchin behavior in the different treatments that would artificially create or mask the effects we are studying?

Cage effects on the physical–chemical environment and thus on urchin behavior could have resulted from interference with water movement, the provision of added environmental heterogeneity and structure, and restriction of the animals' normal movement patterns. We utilized monofilament mesh for the cage walls because it interfered minimally with water movement. Its flexibility also prevented urchins from climbing up the walls, which they did with stiffer materials. We also minimized the cage structure as much as possible to avoid interfering with the natural habitat. Urchins came into contact only with the monofilament mesh wall. They behaved toward the wall as they did toward other habitat structure, i.e. they occasionally sheltered under it. Effects from the cage structure were minimal; we observed no abnormal behavior in the cages by either urchins or predators. Since all cages were identical, and replicates of treatment were performed in different cages, there is no reason to assume any consistent difference between controls and predator treatments.

The key issue is the third one mentioned above, i.e. whether there are interactions between cage effects and urchin behavior in the different treatments that would create or mask the aggregating behavior we were studying. One such potential interaction did concern us. The cages did restrict urchin movement, especially in the high-density treatments in the kelpbed. Without the cages, the urchins would have dispersed. We considered the possibility that urchins clumped in the presence of lobsters only because they had attempted to flee and could not. In a natural situation with widespread high urchin density, however, urchins from a small area would not be able to disperse. As they began to do so, densities would become locally enhanced, and clumping would be speeded because of the density effect. We found, however, that the percent of urchins along the cage wall is completely uncorrelated with mean clump sizes. This indicates that the clumping response, the main focus of interest, acts independently of any dispersal, or wall, effect.

In addition, the results we obtained at Green Island are almost identical to those we obtained in a pilot experiment near Halifax (Tables 7 and 8) where the presence of crabs was associated with significantly larger clumps. Clump sizes were larger in this pilot experiment most probably because there were four large crabs per cage, rather than two. Finally, the clump sizes, and the rapidity of the aggregation response, agree with our laboratory results reported in an earlier study (Bernstein et al. 1981). We are therefore confident that there is no serious bias in our experimental results.

TABLE 7. Treatment means of pilot experiment in the barrens to test for the presence of clumping in the field. Cages were about 1 m^2. *a*, mean clump size; *b*, % clumped.

		Substrate			
		Sand		Rock	
Crabs	Density	*a*	*b*	*a*	*b*
Without	5	2.4	46.7	1.3	40.0
Without	10	2.2	74.0	2.0	65.7
Without	10	1.8	63.3	2.5	76.3
Without	15	1.3	42.0		
With	15	2.7	86.0	3.5	90.7

TABLE 8. Effect of crabs, urchin density, and habitat on mean urchin clump size and % clumped, tested by ANOVA. Clump sizes transformed to $\log_{10}(x + 1)$ of clump size, and % clumped transformed with arc sine square root. $^*P < 0.05$.

Variable	Source	df	Sums of squares	Mean square	*F*
Clump size	Crabs	1	0.45	0.45	5.73*
	Density	2	0.16	0.08	1.01
	Substrate	1	0.01	0.01	0.06
	Residual	19	1.51	0.08	
% clumped	Crabs	1	0.55	0.55	6.44*
	Density	2	0.35	0.18	2.07
	Substrate	1	0.02	0.02	0.18
	Residual	19	1.62	0.09	

AGGREGATION

We found that urchin aggregating behavior is extremely flexible and is responsive to changes in several important environmental parameters. These responses are probably mediated by urchins' sensitivity to biochemical cues. Garnick (1978) has shown that *S. droebachiensis* in the laboratory can consistently discriminate among combinations of cues from other urchins, *Laminaria*, and urchins feeding on *Laminaria*. Urchins respond to these cues by moving toward them, and respond most strongly to other urchins eating *Laminaria*. K. H. Mann and B. E. Welsford (unpublished data) have demonstrated that urchins' behavioral response to *Laminaria* depends on their sensitivity to small, volatile molecules (1000−10 000 MW) released by *Laminaria*. They have also established that *S. droebachiensis* flees from lobster and crab scent in laboratory Y-tube experiments.

This sensitivity allows urchins to respond to changes in their environment that have clear adaptive significance, i.e. the opportunity for increased food, or the risk of increased predation. What the present experiments, as well as our previous work (Bernstein et al. 1981), demonstrate is that the intensity and type of urchin defensive responses to predators are adjusted to the intensity and type of predation. For example, urchins hide when large predatory fish are present, and only form exposed feeding aggregations in the presence of these predators at extremely high densities ($80 \cdot m^{-2}$). Urchins also hide in the presence of lobsters, but will begin forming exposed defensive aggregations when their density surpasses $20 \cdot m^{-2}$. In each instance where aggregations form, their effect is to allow urchins to forage openly while minimizing the risk of predation. We have shown previously (Bernstein et al. 1981) in laboratory experiments that large crabs are much less successful attacking urchin aggregations than they are attacking individual urchins, even when these individuals are well sheltered in rocks. Crabs find it impossible to encircle an aggregation with their claws; in effect, it is one huge urchin. While we have no analogous documentary evidence for lobsters, we hypothesize that aggregations provide urchins with similar protection from lobsters. Aggregation is thus a more effective defence than hiding, because both crabs and lobsters can readily enter the spaces between the boulders.

The formation of these aggregations depends not only on urchin density and predators, but also on habitat type. Urchins aggregate in response to lobsters in the kelpbed, but to crabs in the barrens. This implies that there is some qualitative difference between lobster and crab predation, that perhaps lobsters forage more effectively in kelpbeds, while crabs forage more effectively in the barrens. There is, unfortunately, no detailed information on the relative abundance, microhabitat utilization, or foraging tactics of these two predators in barrens and kelpbed habitats.

COMMUNITY STRUCTURE

The kelpbed−barrens ecosystem exhibits a radical shift between two clear-cut states. The kelpbed state is characterized by persistent and dense cover of the large kelps, *Laminaria* sp., with an understory of *Chondrus* and other forms, and the presence of few sea urchins (*S. droebachiensis*) ($<5 \cdot m^{-2}$) (Mann 1972; Bernstein et al. 1981; Wharton and Mann 1981). The barren state is characterized by an almost complete absence of macroalgae and abundant encrusting coralline algae. Sea urchin densities are much higher than in the kelp ($20-30 \cdot m^{-2}$), and the urchins act to maintain the barrens by grazing any *Laminaria* that resettle (Chapman 1981; Bernstein et al. 1981; Wharton and Mann 1981). There is abundant evidence that dense aggregations of urchins at extremely high densities ($80-100 \cdot m^{-2}$) are the mechanism that transforms the kelpbed into barrens by destructively overgrazing the kelp (Breen and Mann 1976; Mann 1977).

We believe that the experiments described above demonstrate the operation of a behavioral mechanism that is the trigger point for this large-scale change in community structure. Urchins at low density in a healthy *Laminaria* bed remain in hiding. When urchin density passes a critical threshold at about $20 \cdot m^{-2}$, they begin forming small clumps in the open. As lobsters begin feeding on these clumps, urchins' defensive aggregating response precipitates the sudden formation of even larger clumps, destructive grazing of the kelpbed begins, and barrens ultimately form.

Predation has complex effects in this system. Fish, crabs, and lobsters affect the intensity of urchin grazing differently Most importantly, the same predators (lobsters) have completely opposite effects on the intensity of urchin grazing, depending on urchin density. Lobsters have no effect at low urchin density, but catalyze a dramatic aggregation response in the urchins above a threshold density. This defensive clumping is analogous to the formation of flocks or schools in other species (e.g. fish). Defensive aggregating behavior in urchins shifts the relative intensity of the mortality urchins are

exposed to by lowering the intensity of predation. Urchins appear to shift among the several behaviors available to them, based on a combination of conditioning and a rapid response to biochemical cues, including those from algae, predators, and other urchins. This entire process, including its large-scale end result, is therefore understandable in terms of the behavioral responses of individual organisms to immediate selective pressures.

Acknowledgments

We thank Randall Angus, John Stairs, and Solange Brault who carried out the field operations, often under difficult conditions, and Don Peer and Ken Freeman who monitored progress on behalf of the Department of Fisheries and Oceans. We also thank P. K. Dayton and R. T. Paine for helpful comments on the manuscript.

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Contaminant Accumulation and Physiological Response in Rainbow Trout (*Salmo gairdneri*) Reared on Naturally Contaminated Diets

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Juvenile rainbow trout were reared for 24 wk on practical-type diets formulated with fish meals derived from coho salmon (*Oncorhynchus kisutch*) taken from Lake Michigan, Lake Ontario, and the Pacific Ocean. Levels of contaminants (DDT, chlordane, dieldrin, mirex, and PCBs) increased 10-fold from control and Pacific Ocean salmon-based diets to Lake Ontario salmon-based diets. Rainbow trout accumulated contaminants in direct proportion to dietary levels. However, there were no significant differences in the final body weights, feed to gain ratios, or mortality rates of the trout reared on the different test diets. No signs of abnormal behavior or any indication of histopathological abnormalities were observed in any of the fish. There were no signs of thyroid hyperplasia or any significant decline in serum T_3 or T_4 levels with increasing dietary contaminant levels. Therefore, rainbow trout do not appear to have been affected by the uptake and accumulation of contaminants. However, the trout did not appear to regulate their body burden of contaminants; this ultimately could prove to be toxic and may adversely affect the ability of these fish to reproduce and survive. The final concentrations of mirex and PCBs in the Lake Ontario-fed fish exceeded the allowed limits to protect human health; therefore, fish meals produced from Lake Ontario salmon are unsuitable as a source of feed for aquaculture of rainbow trout intended for human consumption.

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De jeunes truites arc-en-ciel ont été maintenues durant 24 semaines à des régimes alimentaires de type pratique à base de farine de poisson préparée à partir de saumons coho (*Oncorhynchus kisutch*) provenant des lacs Michigan et Ontario et de l'océan Pacifique. Les niveaux de contaminants (DDT, chlordane, dieldrine, mirex et PCB) sont 10 fois plus élevés chez les poissons nourris à des régimes à base de saumons du lac Ontario, comparativement

Printed in Canada (J7299)
Imprimé au Canada (J7299)

aux témoins et à ceux nourris à base de saumons provenant du Pacifique. Les truites arc-en-ciel accumulent les contaminants en proportion directe des niveaux dans le régime. Cependant, il n'y a pas de différences significatives de poids somatique final, de rapport nourriture : gain pondéral, ou de taux de mortalité chez les truites élevés aux différents régimes expérimentaux. Nous n'observons, chez aucun poisson, de signes de comportement anormal ou d'anormalité histopathologique. Il n'y a pas d'indice d'hyperplasie thyroïdienne, non plus que d'une diminution significative des niveaux sériques T_3 ou T_4 avec l'augmentation des niveaux de contaminants. La truite arc-en-ciel ne semble donc pas affectée par l'assimilation et l'accumulation de contaminants. Cependant, elle ne semble pas être capable de régler sa charge corporelle de contaminants; ceci peut éventuellement s'avérer toxique et réduire la capacité de reproduction et de survie de ces poissons. Les concentrations finales de mirex et de PCB dans les truites dont la nourriture provient du lac Ontario dépassent les limites maximales permises pour la santé humaine; c'est pourquoi les farines de poisson produites à partir du saumon du lac Ontario ne conviennent pas comme source de nourriture de truites arc-en-ciel d'aquiculture destinées à la consommation humaine.

Received March 15, 1983
Accepted July 27, 1983

Reçu le 15 mars 1983
Accepté le 27 juillet 1983

ECOSYSTEMS of the Great Lakes contain a variety of contaminants, such as mirex and polychlorinated biphenyls (PCBs), which bioconcentrate in fish to levels that are unacceptable for human consumption. These contaminants may also have an effect on other piscivores such as predatory fish. The increasing incidence of thyroid tumors in coho salmon (*Oncorhynchus kisutch*) from the Great Lakes may be a response to their high contaminant concentrations (Sonstegard and Leatherland 1976; Moccia et al. 1977, 1978). Studies on yearling coho salmon fed mirex and PCBs have demonstrated contaminant-induced lowering of serum L-thyroxine (T_4) and triiodo-L-thyronine (T_3) levels (Leatherland and Sonstegard 1977, 1978). However, single or multiple contaminant feeding studies in the laboratory may not adequately reflect the toxicity of complex mixtures of contaminants that fish encounter in the Great Lakes.

Few workers have investigated the effects on fish of consuming diets containing fish from the Great Lakes. Sommer et al. (1982) demonstrated that perch (*Perca flavescens*) fed diets containing fish meal from Lake Michigan alewifes (*Alosa pseudoharengus*) accumulated only small amounts of PCBs in fish fillets, and that after 32 wk of exposure to this diet there were no negative effects on mortality and growth. The ratio of PCBs in fillets to PCBs in the diet was only 0.39, which the authors attributed to the low fat content of perch muscle relative to that of salmonids. These authors concluded that naturally contaminated fish might be a useful protein source for formulating practical fish diets. Leatherland and Sonstegard (1982b) examined the bioaccumulation of organochlorines and their pathophysiological effects in yearling coho salmon reared on diets formulated with beheaded, eviscerated fish from various regions of the Great Lakes and the Pacific Ocean. Despite a significant contaminant accumulation, they observed no significant effect of the complex mixtures of contaminants on the growth and feed efficiency of the salmon. However, there was a significant contaminant effect on salmon thyroid function and on the ability of salmon to mobilize liver glycogen. Therefore, the response of fish to these naturally contaminated diets may vary with the species tested and their ability to metabolize and excrete contaminants.

This study was undertaken to determine (1) the physiological response of juvenile rainbow trout reared on practical-type trout diets formulated with naturally contaminated fish meals and (2) the accumulation of contaminants by trout from naturally contaminated diets.

Materials and Methods

GENERAL DESIGN

Four practical trout diets were formulated using fish meals derived from coho salmon that had been caught in the Pacific Ocean, Lake Michigan, or Lake Ontario (two diets). A fifth diet using commercially prepared capelin (*Mallotus villosus*) meal (from the Atlantic Ocean) was formulated as a control. The diets were fed to four groups of 70 juvenile trout per replicate group for 24 wk. The physiological responses and contaminant accumulation in the trout were monitored after the test period.

DIET PREPARATION AND PROCESSING

Coho salmon collected from the Pacific Ocean (whole), Lake Michigan (degutted), and Lake Ontario (whole) during the 1979 spawning run were frozen at −20°C for approximately 6 mo. The Lake Ontario salmon were divided in two groups: one degutted for direct comparison with the Lake Michigan fish and the other left whole as a comparison with the Pacific Ocean fish. The four groups of salmon were individually ground into fish mash and processed into fish meal and stig-water-oil using a laboratory scale fish processing unit. Water was evaporated from the stig-water-oil to reduce the moisture content by approximately 75%. The stig-water-oil was then remixed with the fish meal. The fish meals were analyzed for ash, moisture, and protein by the method of Horwitz et al. (1970) and for lipid content by the method of Bligh and Dyer (1959). On the basis of the proximate analysis, four test diets, plus one control standard practical diet,

TABLE 1. Percentage composition and proximate analysis of the test diets (results based on the mean of 3 replicates).

	Diet No.				
	1 Control	2 Pacific	3 Michigan	4 Ontario degutted	5 Ontario whole
Ingredient					
Fish meal (+ stig-oil)	—	50	50	50	50
Capelin meal	38	—	0.8	5.3	1.5
Soybean meal	20	—	—	—	—
Gelatin	—	3.8	3.8	3.8	3.8
Wheat middlings	31	30.6	29.8	30.6	35.1
Vitamin premix[a]	1.6	1.6	1.6	1.6	1.6
Mineral premix[a]	0.8	0.8	0.8	0.8	0.8
Salmon oil	8.6	13.2	13.2	7.9	7.2
Analysis[b]					
Protein (%)	41.9	42.2	41.5	41.2	41.6
Lipid (%)	16.7	17.5	18.3	18.7	17.9
Ash (%)	6.5	6.7	5.8	6.0	5.5
Energy (kJ/g)	21.1	21.4	22.2	21.9	20.9
Moisture (%)	5.1	6.6	5.7	5.8	5.8

[a]Vitamin and mineral premix as given in Cho et al. (1974).
[b]On a dry matter basis.

were formulated to be isonitrogenous and on the basis of the dietary lipid and protein levels of equal energy value (Table 1); this was confirmed by proximate analysis of the five diets. The diets were steam processed into pellets in a laboratory pellet mill (California Pellet Mill Co., San Francisco, CA), dried in a fan-ventilated chamber at room temperature for 24 h, and stored in a cooler (0–5°C) until used.

SUPPLY AND MAINTENANCE OF FISH

Rainbow trout were obtained from a commercial trout farmer (Goosen's Trout Farm Ltd., Otterville, Ont.). After a 2-wk acclimation period, approximately 70 fish were transferred to each of 20 rectangular, enamel-lined metal tanks (capacity 45 L). Each tank was aerated and supplied with charcoal-filtered City of Guelph municipal water at a rate of 2–3 L/min. Water temperature was maintained at 15 ± 0.8°C, the pH varied between 7.7 and 7.9, and the dissolved oxygen varied between 7.2 and 8.6 mg/L throughout the test period. The photoperiod was maintained at 12 h light : 12-h dark with fluorescent lighting in a windowless laboratory.

The test diets were fed to four groups of 70 fish per tank (initial weight 3.7 ± 0.1 g/fish) for 24 wk or six 28-d periods. The fish were fed three to six times daily to satiety (Hilton and Slinger 1981); the size of feed pellets was adjusted after each 28-d period.

GROWTH, PATHOLOGY, AND CONTAMINANT ASSAYS

Body weights, feed to gain ratios, and total mortalities were determined after each 28-d period. After 24 wk on the test diets, fish were selected at random and assayed for the following parameters.

Proximate composition — Two fish from each tank were ground, freeze-dried, and stored at −20°C. The carcass ash (ignition at 600°C), moisture (weight loss at 105°C for 24 h), and crude protein content (N × 6.25) were determined as described by Horwitz et al. (1970) and carcass lipid by the method of Bligh and Dyer (1959).

Ascorbic acid — Liver and head kidney tissues were removed from approximately four fish per tank, frozen with liquid nitrogen, stored at −20°C, and assayed for total ascorbic acid concentration by the method of Aeschbacher and Brown (1972). Diet samples were also assayed for total ascorbic acid content by the same method.

Hematology — Approximately four fish per tank were anaesthetized with tricaine methanesulphonate (MS222, Syndel Laboratories, Vancouver, B.C.) and their blood collected in sodium heparinized tubes after transection of the caudal peduncle. The blood was immediately centrifuged and the plasma stored at −20°C until required for analysis. Plasma glucose was determined by the glucose oxidase method (Boehringer-Mannheim Kit No. 166 391, Dorval, Que.), and plasma protein was determined by the method of Lowry et al. (1951). Hemoglobin concentrations were determined on a further 10 fish per treatment by the cyanmethemoglobin method (Unopette test 5857, Becton, Dickinson and Co. Ltd., Mississauga, Ont.) and hematocrits were measured using heparinized microhematocrit tubes.

Thyroid hormones — A further 10 fish per treatment were removed and the blood was collected without heparin. After coagulation, the serum was stored at −20°C. Serum T_4 and T_3 levels were measured by radioimmunoassay (Miles Laboratories, Toronto); intra- and inter-assay coefficients of variation were less than 10% ($N = 12$), and there was good parallelism between serum volume and the standard curve.

TABLE 2. Final body weight, feed to gain ratio, mortalities, and final carcass proximate composition of the trout after 24 wk on the test diets (results based on the mean of 4 replicates ± SD).

	Diet No.				
	1 Control	2 Pacific	3 Michigan	4 Ontario degutted	5 Ontario whole
Body weight (kg/100 fish)[a]	13.6±0.7	11.8±0.4	14.1±0.9	12.4±0.6	13.2±0.6
Feed to gain	1.1±0.2	1.1±0.2	1.1±0.1	1.1±0.1	1.1±0.1
Mortalities[b]	0.1	0.2	0	0	0.2
Analysis (%)					
Protein	52.0±2.6	53.5±1.5	50.3±1.1	51.0±1.8	49.2±3.4
Lipid	38.8±2.5	35.4±5.2	41.4±2.3	40.3±2.6	41.6±1.5
Dry matter	32.5±1.1	30.7±0.7	32.8±0.7	31.4±1.5	31.9±1.0
Ash	9.8±1.3	11.1±2.8	8.5±0.8	8.5±0.4	8.1±0.3

[a]Initial weight 3.7 ± 0.1 g/fish.
[b]Number of mortalities per 10 000 fish-days (total fish-days varied between 37 904 and 41 730).

Histopathology — Three fish from each tank were chosen at random and killed by severing the spinal cord behind the head. The anterior and posterior kidney, liver, thyroid, spleen, and dorsal body wall musculature were immediately removed, fixed in 10% buffered formalin, and stored in 70% ethyl alcohol. The tissues were examined histopathologically by the Veterinary Services Branch, Department of Pathology, University of Guelph.

Contaminants — Two fish per tank were ground and frozen at −20°C until required for analysis. Fish mash, fish meal, stig-water-oil, final test diet, and frozen carcass mash were also assayed for organochlorine insecticides, hexachlorobenzene (HCB), and polychlorinated biphenyls (PCBs) according to the procedure described by Frank et al. (1978).

Statistical Analysis

The data were separately subjected to a one-way analysis of variance. Where F values indicated significance, the means were compared using Tukey's honestly significant difference procedure (Steel and Torrie 1980).

Results

Growth and Biochemical Parameters

There were no differences ($P > 0.05$) in the weight gain, feed to gain ratios, or mortality rates of the trout after 24 wk on the test diets (Table 2). No overt signs of toxicity, or any abnormal behavior, were observed in any of the trout. No differences ($P > 0.05$) were detected in the final carcass composition of the trout (Table 2) after 24 wk on the test diets.

The ascorbic acid content of the control diet and Pacific salmon-based diet were higher ($P < 0.05$) than the Lake Michigan and two Lake Ontario salmon-based diets (Table 3). The ascorbic acid contents of the head kidney and livers were also higher ($P > 0.05$) in trout reared on the control and Pacific diet than trout reared on the Lake Michigan and Lake Ontario diets.

No significant differences were detected in the plasma glucose, plasma protein, hemoglobin, and hematocrit levels of the trout after 24 wk on the different test diets (Table 4). Serum T_4 levels were significantly higher in trout reared on the Lake Ontario whole diet than in trout from the other four groups, with the lowest T_4 levels occurring in trout reared on the Pacific diet. Trout reared on the Pacific diet had significantly lower serum T_3 levels than trout reared on the control, Lake Michigan, and Lake Ontario whole diets (Table 4).

Histopathology

No gross external lesions were apparent on the fish or on any of the internal organs of the trout after 24 wk on the test diets. No significant pathological changes were apparent in any of the tissues examined (muscle, kidney, liver, spleen, and thyroid).

Pesticide Analysis

The pesticide content of the fish mash, fish meal, and stig-water-oil was highest in the Lake Ontario whole salmon and lowest in the Pacific salmon (Table 5). The control diet had slightly lower pesticide levels than the Pacific diet, and both of these diets had approximately 1/10 the pesticide content of the Lake Michigan and Lake Ontario salmon-based diets. The process of making fish meal from the raw mash caused a slight increase in contaminant concentrations on a wet weight basis, while the removal of water to produce a "dry pellet" dramatically increased contaminant concentrations (Table 5). Final carcass pesticide levels increased in proportion to increased dietary pesticide content (Table 5). The concentration factor of DDT, chlordane, dieldrin, and PCBs were either essentially the same or increased from the control group to the Lake Ontario whole group (Table 6). Similarly, the mass balance of each pesticide was also either essentially the same or increased from the control group to the Lake Ontario whole diet-fed group, with the exception of the dieldrin mass balance in the Lake Michigan diet-fed group.

TABLE 3. Ascorbic acid content (μg/g) of the head kidney, liver, and test diets (results based on the means of 4–8 replicates ± SD). Values followed by the same letter not significantly different ($P > 0.05$).

	Diet No.				
	1 Control	2 Pacific	3 Michigan	4 Ontario degutted	5 Ontario whole
Liver	94.0±18.0a	71.9±19.0a	49.6±9.6b	46.9±15.8b	48.5±10.8b
Head kidney	183.1±22.4a	143.7±13.0ab	114.2±32.0b	97.2±40.7b	85.4±20.6b
Diet	90.3±4.7a	81.5±4.4a	62.8±2.0b	52.8±6.5b	67.2±0.9b

TABLE 4. Plasma glucose, plasma protein, hemoglobin, hematocrit, T_4, and T_3 levels of the trout after 24 wk on the test diets (results based on the mean of 10–16 replicates ± SD). Values followed by the same letter not significantly different ($P > 0.05$).

	Diet No.				
	1 Control	2 Pacific	3 Michigan	4 Ontario degutted	5 Ontario whole
Plasma glucose (mg/dL)	62.9±5.1	71.7±7.9	62.5±5.4	56.0±5.9	57.8±6.2
Plasma protein (mg/mL)	38.2±4.2	37.5±4.2	38.4±2.9	37.1±3.5	39.2±3.5
Hemoglobin (g/100 mL)	7.5±0.5	8.5±0.5	8.4±9.8	8.1±0.5	7.9±0.6
Hematocrit (%)	37.0±2.5	39.5±2.6	40.5±2.7	37.1±3.1	37.1±1.4
Serum T_4 (μg/dL)	0.51±0.19a	0.39±0.06a	0.46±0.09a	0.47±0.16a	0.71±0.19b
Serum T_3 (μg/dL)	0.54±0.11a	0.37±0.06b	0.51±0.07a	0.47±0.15ab	0.58±0.07a

Discussion

Our experiment demonstrated that feeding trout on naturally contaminated diets produced no measurable adverse responses. There was, however, significant contaminant accumulation, which was in direct proportion to the levels of contaminants in the diets. This lack of physiological response was not surprising. The results support those of Sommer et al. (1982) and to a certain extent those of Leatherland and Sonstegard (1982b) who observed no effects of naturally contaminated diets on the growth and mortality of perch and coho salmon, respectively. In contrast, rats fed naturally contaminated coho salmon from Lakes Ontario, Erie, and Michigan showed growth retardation, thyroid enlargement (both hypertrophy and hyperplasia), and reduced levels of T_4 relative to those fed Pacific salmon or rat chow (Sonstegard and Leatherland 1978, 1979; Leatherland and Sonstegard 1980, 1982a). The thyroid enlargement was unresponsive to iodine supplementation, suggesting that the cause was not iodine deficiency. These observations are analogous to thyroidal pathology of coho salmon from the Great Lakes (Sonstegard and Leatherland 1976; Moccia et al. 1978, 1981) and, to some extent, coho salmon fed naturally contaminated diets (Leatherland and Sonstegard 1982b).

It is possible that rats and coho salmon are more sensitive to contaminants than are trout. Alternatively, differences in feed quality, stress, or feed preparation techniques may have influenced the outcome of the feeding experiments. The rats in the studies by Sonstegard and Leatherland (1978, 1979) were fed salmon that were eviscerated, beheaded, homogenized, and stored frozen until consumed without any additional nutrient supplementation. A subsequent experiment in which rats were fed nutritionally complete diets containing up to 5.8% freeze-dried Lake Ontario or Pacific salmon showed that the growth effect may be due to palatability (Villeneuve et al. 1981). However, rats in this latter study showed elevated activities of mixed function oxidase enzymes, a direct response to the contaminants in the diet. In the present study, and that of Sommer et al. (1982), fish meal was produced by processes involving heat, and the fish meal was only a part (50%) of the final product that contained supplements of vitamins and minerals plus sufficient added fish meal, fish oil, and wheat middlings to make all diets isonitrogenous and of equal energy value.

It is well known that the addition of heat, steam, and pressure during processing can adversely affect the nutrient quality of protein sources such as fish mash or meal. In this respect it is interesting to note that the PCB levels declined from the fish mash to fish meal in groups 2 through 5; therefore, some loss or destruction of PCBs obviously occurred during processing. It is difficult to determine whether the same proportion or percentage losses of PCBs occurred in all the groups, and this should be investigated in future research. In contrast, total DDT levels appeared to be unaffected by the processing methods. It is of interest that the Pacific salmon-based diet (group 2, Table 1) had the lowest contaminant levels, being almost as low as those in diet 1, the control diet. Considering that diet 1 contained 15% less fish meal (from capelin) in the diet formulation, it is probable that both diets 1 and 2 would have had virtually the same contaminant levels if diet 2 contained the same level of fish meal (from salmon) as diet 1. The diets were essentially isonitrogenous and of approximately equal energy value; therefore, these

TABLE 5. Contaminant content of the fish mash, fish meal, stig-water-oil, test diets, and final fish carcass of the trout after 24 wk on the test diets (carcass analysis based on the mean of four fish per treatment ± SD). Tr, trace; ND, not detected.

		Contaminant (μg/g)											
Diet	Sample	ΣDDT	*pp*-DDE	*pp*-TDE	*pp*-DDT	*op*-DDT	Dieldrin	Heptachlor epoxide	α-BHC	Chlordane	HCB	PCB	Mirex
1	Diet (dry wt)	0.07	0.02	0.03	0.02	ND	0.00	0.00	Tr	0.01	ND	0.1	ND
Control	Carcass (dry wt)	0.14±0.03	0.04±0.01	0.06±0.01	0.04±0.01	ND	0.01±0.00	ND	ND	0.03±0.00	ND	0.24±0.03	ND
2	Fish mash (wet wt)	0.01	0.01	Tr	Tr	ND	Tr	Tr	ND	0.00	ND	0.03	ND
Pacific	Fish meal (wet wt)	0.02	0.02	ND	ND	ND	0.00	0.00	ND	ND	ND	ND	ND
	Stig-water (μg/L)	Tr	Tr	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Diet (dry wt)	0.11	0.03	0.05	0.03	ND	0.01	0.00	0.01	0.02	ND	0.10	ND
	Carcass (dry wt)	0.22±0.03	0.21±0.06	0.09±0.02	0.05±0.02	ND	0.01±0.00	ND	ND	0.03±0.00	ND	0.27±0.04	ND
3	Fish mash (wet wt)	0.33	0.29	0.02	0.02	ND	0.02	0.004	ND	0.048	Tr	1.7	ND
Michigan	Fish meal (wet wt)	0.46	0.42	0.04	ND	ND	0.05	0.01	ND	0.09	ND	0.08	ND
	Stig-water (μg/L)	0.02	0.02	ND	ND	ND	0.01	0.01	ND	ND	ND	0.03	ND
	Diet (dry wt)	1.16	0.80	0.31	0.06	ND	0.05	0.01	0.01	0.04	ND	1.27	ND
	Carcass (dry wt)	2.62±0.18	1.88±0.38	0.03±0.00	0.11±0.03	ND	0.10±0.00	0.01±0.00	ND	0.21±0.06	ND	4.42±0.32	0.11±0.04
4	Fish mash (wet wt)	0.25	0.19	0.02	0.03	0.01	0.06	0.01	ND	0.04	0.01	6.0	ND
Ontario	Fish meal (wet wt)	0.96	0.75	0.14	0.03	0.04	0.11	0.02	ND	0.16	ND	1.86	ND
degutted	Stig-water (μg/L)	0.13	0.11	0.02	ND	Tr	0.08	0.02	ND	0.02	ND	0.50	ND
	Diet (dry wt)	1.39	0.75	0.47	0.17	ND	0.07	0.01	0.01	0.04	ND	2.12	0.11
	Carcass (dry wt)	5.22±0.49	2.85±0.27	1.76±0.18	0.61±0.08	ND	0.20±0.04	0.03±0.01	ND	0.32±0.08	ND	8.69±0.48	0.33±0.06
5	Fish mash (wet wt)	0.15	0.12	0.01	0.01	0.01	0.06	0.01	ND	0.03	0.01	4.2	ND
Ontario	Fish meal (wet wt)	1.47	1.11	0.25	0.04	0.07	0.18	0.02	ND	0.24	ND	2.17	ND
whole	Stig-water (μg/L)	0.14	0.11	0.03	ND	Tr	0.21	0.03	ND	0.03	ND	0.91	ND
	Diet (dry wt)	2.10	1.06	0.74	0.24	ND	0.11	0.01	0.01	0.15	ND	3.60	0.16
	Carcass (dry wt)	5.36±0.64	2.67±0.32	2.19±0.32	0.50±0.06	ND	0.23±0.02	0.02±0.01	ND	0.29±0.02	ND	7.62±0.86	0.25±0.07

TABLE 6. Concentration factor (CF, tissue contaminant concentration ÷ dietary contaminant concentration) and mass balance (MB, 100 × (contaminant content per fish ÷ total contaminant level consumed per fish)) of the trout after 24 wk on the test diets.

		Diet No.				
Contaminant	Parameter	1 Control	2 Pacific	3 Michigan	4 Ontario degutted	5 Ontario whole
ΣDDT	CF	2.0	2.1	2.3	3.8	2.6
	MB	60.2	59.3	69.3	110.3	75.9
Chlordane	CF	3.1	2.1	5.0	7.3	2.0
	MB	94.3	59.4	70.1	100.6	58.5
Dieldrin	CF	3.0	1.3	2.2	2.9	2.2
	MB	92.2	37.7	21.6	84.4	64.1
PCB	CF	2.2	2.7	3.5	4.1	2.1
	MB	66.1	48.7	106.7	120.4	63.3

factors should not have confounded the results of the study. It is obvious, however, that further research is required on the effect of processing methodology (particularly cooking) on the toxicity of Great Lakes fish to mammals and fish.

Previous research has shown that ascorbic acid increases the metabolism and excretion of contaminants such as PCBs (Kato et al. 1977) and toxaphene (Mayer et al. 1978). Therefore, it is possible that the reduction in tissue ascorbic acid levels that we found (Table 3) indicates enhanced utilization of this vitamin for contaminant excretion. However, dietary levels of the vitamin were also lower in the high contaminant level diets, despite the fact that ascorbic acid was supplemented at the same level (400 mg/kg diet) in all test diets. The probable explanation for this was that the salmon-based diets had a higher moisture content due to the addition of the stig-water-oil. Previous research has shown that excess moisture in a diet, especially during processing, can accelerate the oxidation and destruction of ascorbic acid (Hilton et al. 1977a). The lower dietary levels of ascorbic acid in the salmon-based diets were probably the result of increased destruction of this vitamin during processing. Despite this reduction in dietary and tissue levels of ascorbic acid, the levels found were still well above the acceptable minimum levels of this vitamin required for rainbow trout (Hilton et al. 1977b, 1978). Therefore, the trout appeared to be unaffected by the consumption and accumulation of the different levels of contaminants (Table 6).

The concentration factor and the mass balance of the contaminants (Table 6) do not appear to have been affected by increased dietary contaminant levels. This would indicate that there was no apparent regulation of the contaminants by trout. This lack of regulation could be very serious. While the contaminant levels of the diets in this experiment may have been too low to elicit a response in the trout, they are considered, nevertheless, to be typical of average concentrations for fish from their respective origins. Without regulation, these contaminants could ultimately accumulate to the point where toxicity to fish would be obvious. The absence of any apparent contaminant regulation in the trout may also indicate that the trout is storing these lipophilic compounds in their fat depots. It is possible that only during periods of prolonged fasting and/or starvation, typical of migration and/or reproduction, when lipid stores are mobilized, would these accumulated contaminants have any physiological effect. Mink reared on naturally contaminated fish-based diets had significantly higher mortality rates and reproductive failures than mink reared on control diets (Gilbert 1969; Aulerich et al. 1973). The effects on reproduction may be due to interference in hormone cycles as a result of induction by contaminants of mixed function oxidase enzymes, as observed by Villeneuve et al. (1981). Therefore, it is possible that these accumulated contaminants in the trout may well adversely affect their survival and/or ability to successfully reproduce. This experiment did not measure other subtle toxic effects on the ability of the trout to sexually mature and reproduce, to capture prey and avoid predation, and to resist other stresses such as disease, temperature flux, low dissolved oxygen, etc.

The final concentrations of contaminant residues in the experimental fish were quite high; in the case of Lake Ontario-fed fish, PCBs and mirex, on a wet weight basis, exceeded the limits of 2.0 and 0.1 μg/g, respectively, prescribed to protect human health (Great Lakes Water Quality 1977). Therefore, it is obvious that naturally contaminated diets are unsuitable as a source of feed for aquaculture of rainbow trout intended as food for human consumption. Processes that remove contaminants from fish products, e.g. solvent extraction to produce fish protein concentrate (Power 1962), may provide a solution to this problem. In the meantime, fish from contaminated portions of the Great Lakes will provide a useful source of nutrition only for those fish species that have low muscle fat content, as demonstrated for perch by Sommer et al. (1982).

In view of the suggestions of Sommer et al. (1982) that contaminated fish might be useful as fish feed, further longer term research is needed to ensure no adverse effects on aquaculture.

Acknowledgments

We gratefully thank Gary Chapman, Debbie Conrad, Louise Desjardins, Caryl Morito, Martin Hodgson, Roman Lanno, and Lucy Lin for technical support; Bob Gehl, Tempo-Tech Industries, Hart, MI, Dave Wilson, Department of Fisheries and Oceans, Vancouver, B.C., Bob Stanton, Capilano Hatchery, West Vancouver, B.C., and Mike Whittle, Great Lakes Biolimnology

Laboratory, Department of Fisheries and Oceans, Burlington, Ont., for their invaluable assistance in locating and providing coho salmon; Dave Higgs, West Vancouver Laboratory, Department of Fisheries and Oceans, West Vancouver, B.C., for processing the fish mash into fish meal; Hoffman–La Roche Canada Ltd. for generously donating the vitamins used in this study, and the Natural Sciences and Engineering Research Council of Canada, the Ontario Ministry of Agriculture and Food, and the Ontario Ministry of Natural Resources for financial support.

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Geothermal Effects on Stream Benthos: Separate Influences of Thermal and Chemical Components on Periphyton and Macroinvertebrates

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LAMBERTI, G. A., AND V. H. RESH. 1983. Geothermal effects on stream benthos: separate influences of thermal and chemical components on periphyton and macroinvertebrates. Can. J. Fish. Aquat. Sci. 40: 1995–2009.

Stream microcosms were used in situ to evaluate the separate effects of the thermal and chemical components of geothermal fluids from natural hot springs (which simulate accidental releases from geothermal energy developments) on benthic microorganisms and macroinvertebrates of Big Sulphur Creek, a third-order stream at The Geysers, Sonoma Co., California, USA. The thermal component of geothermal fluids had greater influence than the chemical component in determining benthic community features in Big Sulphur Creek. A natural input of geothermal fluids to Big Sulphur Creek, which elevated both temperature (by 7.5°) and chemical levels (e.g. boron by 10 times, NO_3-N by 4 times, PO_4-P by 2 times), increased benthic chlorophyll *a* by 40 times, bacterial numbers by 10 times, and macroinvertebrate density by 2 times. The stream microcosms showed that heating of nongeothermal water by 8° (i.e. thermal exposure alone) similarly increased chlorophyll *a* by 40 times and bacterial numbers by 2 times, but macroinvertebrate density declined by one fourth. Cooling of geothermal water by 14.5° (i.e. chemical exposure alone) reduced algal productivity but increased macroinvertebrate density by 70 times. Naturally occurring geochemical concentrations apparently can be tolerated by many aquatic organisms in Big Sulphur Creek, but changes in water temperature significantly alter benthic community structure.

LAMBERTI, G. A., AND V. H. RESH. 1983. Geothermal effects on stream benthos: separate influences of thermal and chemical components on periphyton and macroinvertebrates. Can. J. Fish. Aquat. Sci. 40: 1995–2009.

Des microcosmes de cours d'eau ont été utilisés in situ pour évaluer les effets séparés des composantes chimiques et thermiques de fluides géothermiques provenant de sources thermales (ressemblant à des dégagements accidentels lors de développements d'énergie géothermique) sur les micro-organismes et les macro-invertébrés benthiques du ruisseau Big Sulphur, un cours d'eau de troisième ordre de The Geysers, dans le comté de Sonoma, en Californie (É.-U.). La composante thermique des fluides géothermiques a une plus grande influence que la composante chimique sur la détermination des caractéristiques des communautés benthiques de ce ruisseau. Une arrivée naturelle de fluides géothermiques dans le ruisseau, qui cause une élévation à la fois de la température (de 7,5°) et des substances chimiques (p. ex., le boron, de 10 fois; le NO_3-N, de 4 fois; le PO_4-P, de 2 fois), a pour effet d'augmenter la chlorophylle *a* de 40 fois, les nombres bactériens de 10 fois et la densité des macro-invertébrés de 2 fois. Les microcosmes du cours d'eau indiquent que le réchauffement d'une eau non géothermique de 8° (c.-à-d. une exposition thermique seule) augmente aussi la chlorophylle *a* de 40 fois et les nombres bactériens de 2 fois, mais cause une diminution de densité des macro-invertébrés d'un quart. Le refroidissement de l'eau géothermique de 14,5° (c.-à-d. une exposition chimique seule) diminue la productivité algale, mais augmente la densité des macro-invertébrés de 70 fois. Plusieurs micro-organismes du ruisseau Big Sulphur semblent tolérer des concentrations géochimiques naturelles, mais des changements de température de l'eau modifient de façon significative la structure des communautés benthiques.

Received April 22, 1983
Accepted July 29, 1983

Reçu le 22 avril 1983
Accepté le 29 juillet 1983

Printed in Canada (J7334)
Imprimé au Canada (J7334)

GEOTHERMALLY influenced habitats occur worldwide (Waring 1965), but the development of geothermal resources for energy production is limited to relatively few areas (Rinehart 1980). In North America, geothermal resources mainly occur in the western states and provinces (Tillman 1980), and the largest geothermal energy development in the world is located at The Geysers in northern California, USA. Originally developed in the 1930s, The Geysers currently provides over 5% of California's electrical power, an amount equivalent to San Francisco's entire needs. However, the full development of geothermal resources at The Geysers and in other areas has been delayed because of potential environmental impact, especially on aquatic biota (Suter 1978; Katz 1981; Resh et al. 1981). Aquatic habitats may be severely affected by effluents from geothermal operations, particularly the uncontrolled releases of geothermal fluids that result from well blowouts, pipeline ruptures, and sump overflows.

The effects of such development-related disruptions can be predicted by using natural hot springs as model ecosystems (Brock 1967, 1970), since these springs frequently add substantial amounts of heat energy, chemical substances, and water to nongeothermal aquatic habitats (Rinehart 1980). Consequently, such habitats simulate many of the important features of accidental releases of geothermal effluents (Jones 1966). In North America, the ecology of natural geothermal habitats has been most intensively studied in Yellowstone National Park, USA (see Brock 1975, 1978 and references therein). These studies, along with those conducted in other areas (see review by Brock 1970), have shown that the water of geothermal habitats has two important components: high temperature and unique geochemistry; each of these may influence the variety and types of organisms that can live in those habitats.

Unfortunately, nearly all studies of the influences of geothermal fluids on aquatic biota have failed to distinguish between the separate effects of the thermal and the chemical components. For example, when Armitage (1958) and Vincent (1967) reported that the biomass of aquatic insects in the Firehole and Gibbon Rivers in Yellowstone National Park greatly increased below geothermal effluents, they attributed this increase to chemical enrichment (e.g. higher alkalinity due to bicarbonate input) that stimulated the growth of the insects' food (algae and other microorganisms). However, they considered a priori that the concomitant increase in temperature was only of secondary importance.

Both the thermal and chemical components of geothermal fluids have been suggested to be the primary determinants of microbial communities. For example, in geothermal habitats of New Zealand and Iceland, sulfide concentration, and not temperature, was considered to determine algal species composition (Castenholz 1976). In contrast, Boylen and Brock (1973) reported that thermal enrichment was primarily responsible for an increase in algal standing crop that occurred below geothermal additions to the Firehole River, even though higher concentrations of nutrients also occurred downstream of such inputs. In this habitat, temperature was also considered to be important in determining the distribution and growth rates of bacteria (Zeikus and Brock 1972).

Based on such a variety of information about the effects of the different components of geothermal fluids on benthic macroinvertebrates and microorganisms, Brock (1978) emphasized that future biological studies should distinguish between chemical and thermal influences. In addition to establishing tolerance levels of specific taxa to geothermally generated heat and chemicals, such information may be used to develop mitigation procedures that can be concentrated on the component that has the most pronounced impact.

At The Geysers, we determined the combined and separate influences of the thermal and chemical components of geothermal fluids on stream biota by using both descriptive and experimental approaches. First, we designed an "in-stream" study to compare benthic communities in adjacent stream segments that were either influenced or not influenced by geothermal fluids. Second, we developed a field-based "stream microcosm" system that experimentally separated the effects of the thermal and chemical components of geothermal fluids on the benthic community. Using these two designs, we evaluated the responses in the numerical abundance of benthic bacteria, the standing crop and productivity of attached algae, and the density, standing stock, and community structure of benthic macroinvertebrates.

Study Area

This research was conducted in Big Sulphur Creek, Sonoma Co., California, USA (38°47′N, 122°47′W; elev. 670 m), a third-order stream that flows northwesterly through The Geysers–Known Geothermal Resources Area (Fig. 1A, 1B). The drainage basin of Big Sulphur Creek is formed by a steeply sided valley in the Mayacmas mountain range of northern California. Vegetation is that of a mixed-species evergreen forest, dominated by Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and oaks (*Quercus* spp.). Precipitation occurs primarily as rain ($\bar{x}$ = 137 cm/yr), 95% of which falls between November and April.

Our principle study site was at the confluence of Big Sulphur Creek and its tributary, Little Geysers Creek (Fig. 1C). Big Sulphur Creek is a cold (i.e. nongeothermal) stream above the confluence; Little Geysers Creek is a heated (i.e. geothermal) stream formed by a number of small hot springs that issue from the banks and the streambed. Although the discharge volume of Little Geysers Creek is usually only about one-third that of Big Sulphur Creek, this geothermal tributary raises water temperature in Big Sulphur Creek an average of 7.5° during the spring and summer. This input also increases the concentrations of several chemical substances in Big Sulphur Creek (Fig. 2). For example, boron concentration increases by more than 10 times (from <0.1 to 1.2 mg/L), NO_3-N increases almost 4 times (from 0.03 to 0.11 mg/L), and PO_4-P increases 2 times (from 0.01 to 0.02 mg/L). The influence of the thermal and chemical inputs to Big Sulphur Creek is apparent for 250 m below the confluence. Below this point, smaller hot springs empty into Big Sulphur Creek and result in additional, but more localized, geothermal influences throughout the stream's length.

Experimental Design

We conducted the in-stream study to compare benthic communities in Big Sulphur Creek (BSC) at two sites: 100 m upstream and 50 m downstream of the geothermal input from Little Geysers Creek (LGC). These sites were selected

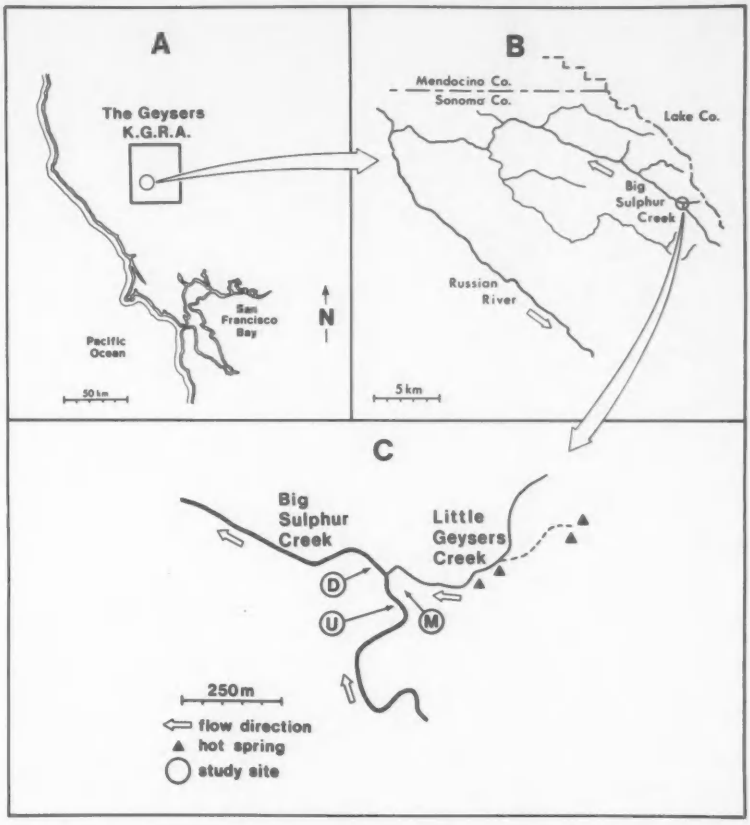

FIG. 1. Study area. (A) The Geysers–Known Geothermal Resources Area (K.G.R.A.) in relation to San Francisco Bay, CA; (B) major aquatic habitats in the principal development area at The Geysers; (C) study area and sampling sites at the confluence of Big Sulphur Creek (BSC) and Little Geysers Creek (LGC). U, BSC-upstream; D, BSC-downstream; M, location of stream microcosms.

because they were the closest areas to the confluence that had similar physical characteristics, such as water depth, current velocity, substrate composition, and illumination. Benthic macroinvertebrates and microorganisms were sampled using unglazed red clay tiles (each 15.2 × 7.6 cm) that were placed directly on the substrate. On 1 June 1979, 36 tiles were arranged in a 6 × 6 grid at each site in a shallow riffle that was moderately shaded by streamside vegetation. Five tiles were collected weekly at random from each site for 7 consecutive wk, ending 18 July 1979; the abundances of benthic bacteria, algae, macroinvertebrates, and total organic matter were determined for each tile.

We constructed four stream microcosms near the confluence of BSC and LGC (Fig. 3A) to assess the separate effects of the thermal and chemical components of those geothermal fluids from LGC on benthic biota. The four microcosms used in this study (Fig. 3B) were as follows: (1) control: no thermal or chemical influence, water source was BSC upstream of LGC; (2) thermal plus chemical (T + C): both thermal and chemical influences, water source was LGC; (3) thermal: thermal influence only, cold water from BSC upstream of LGC was heated using hot water from LGC in a heat-exchange system; (4) chemical: chemical influence only, hot water from LGC was cooled using cold water from BSC in a second heat exchanger.

Water was transported by gravity (2 m of hydraulic head) from the two sources, BSC and LGC, to the site of the microcosms in a 7.6-cm-diameter flexible styrene pipe. Each microcosm was a plexiglass trough (0.9 × 0.3 × 0.13 m deep) with an open top (Fig. 3A); all fittings between the pipes and the microcosms were made of polyvinyl chloride (PVC). Water flowed through the microcosm only once and was then released into BSC.

All four microcosms were identical, except that the thermal microcosm was fitted with a specialized compartment at the input end that contained the heat-exchange system and

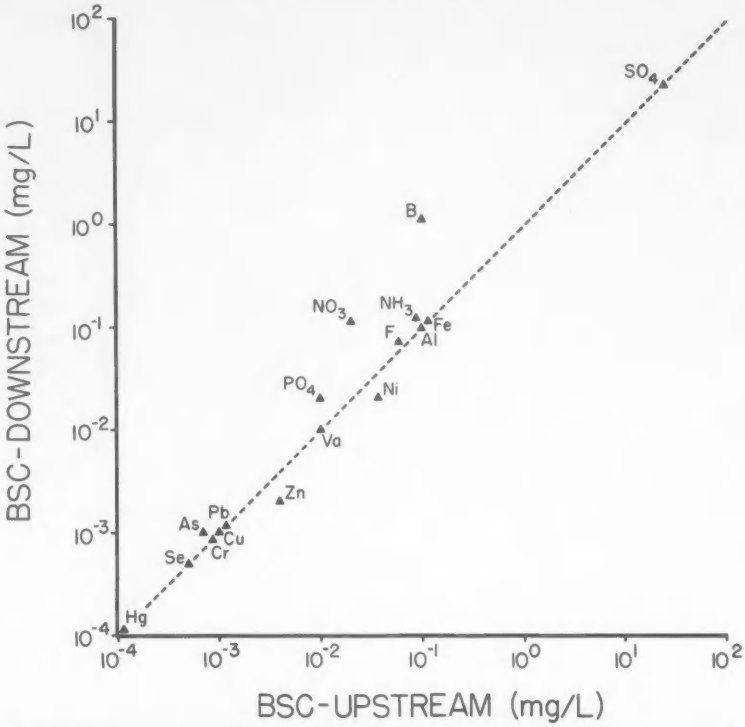

FIG. 2. Comparison of chemical concentrations in Big Sulphur Creek (BSC) at 100 m upstream (BSC-upstream) and 50 m downstream (BSC-downstream) of Little Geysers Creek (LGC) on 6 May 1981. Points along broken line indicate equal concentrations at BSC-upstream and BSC-downstream; points above the line indicate higher concentrations at BSC-downstream, a result of chemical inputs from LGC to BSC; points below the line indicate higher concentrations at BSC-upstream, a result of dilution by LGC; pH = 7.6 at both sites.

produced the thermal treatment (Fig. 3). This closed compartment contained 100 thin-walled aluminum tubes (30 cm long, 0.6 cm in diameter) through which hot water from LGC continually flowed. Cold water from BSC passed over the tubes and was heated without adding geothermal chemicals before it entered the thermal microcosm.

To produce the chemical treatment, six aluminum coils, each consisting of 18 tubes (60 cm long, 1.0 cm in diameter) connected by vinyl tubing, were submerged in the cold section of BSC. Hot water from LGC circulated through the coils and was cooled, while still retaining its chemical constituents, before being delivered to the chemical microcosm. No chemical precipitates were ever observed in the water of the chemical microcosm, which indicates that the cooling process did not reduce chemical concentrations.

Most of the materials used to construct the microcosms (e.g. styrene, PVC, plexiglass) are relatively inert. However, we were concerned about potential contamination by aluminum from the tubes used in the heat-exchange units of the thermal and the chemical microcosms. Total aluminum concentration in the water was measured in each of the four microcosms at the end of the 34-d study period but was undetectable (i.e. <0.1 mg/L) in each case.

A sterilized mixture of BSC stream gravel consisting of 1 L (volumetric displacement) each of three substrate size categories, 2–4, 4–8, and 8–16 mm, was added to each microcosm (depth of substrate = 2.5 cm). Fourteen tiles (each 7.6 × 7.6 cm) were placed on top of the substrate in each microcosm. The microcosms were operated for a 34-d period, 9 June–13 July 1981. We maintained discharge at 0.1 L/s and water depth at 6 cm in each microcosm throughout the study period. Three tiles were randomly collected from each microcosm (and replaced by new tiles) after exposures of 3, 6, 11, 21, and 34 d (the 15th tile was part of the replacement set for day 3). These tiles were used to analyze benthic bacteria, algae, and total organic matter. After collecting the final set of tiles (13 July 1981), the entire substrate from each 0.22-m^2 microcosm was collected and preserved to inventory the benthic macroinvertebrate community.

We monitored water temperature for each microcosm with maximum–minimum thermometers that were read every 1–2 d. Dissolved oxygen concentration, pH, and conductivity in each microcosm were measured at midday (12:00–14:00) every 3–4 d.

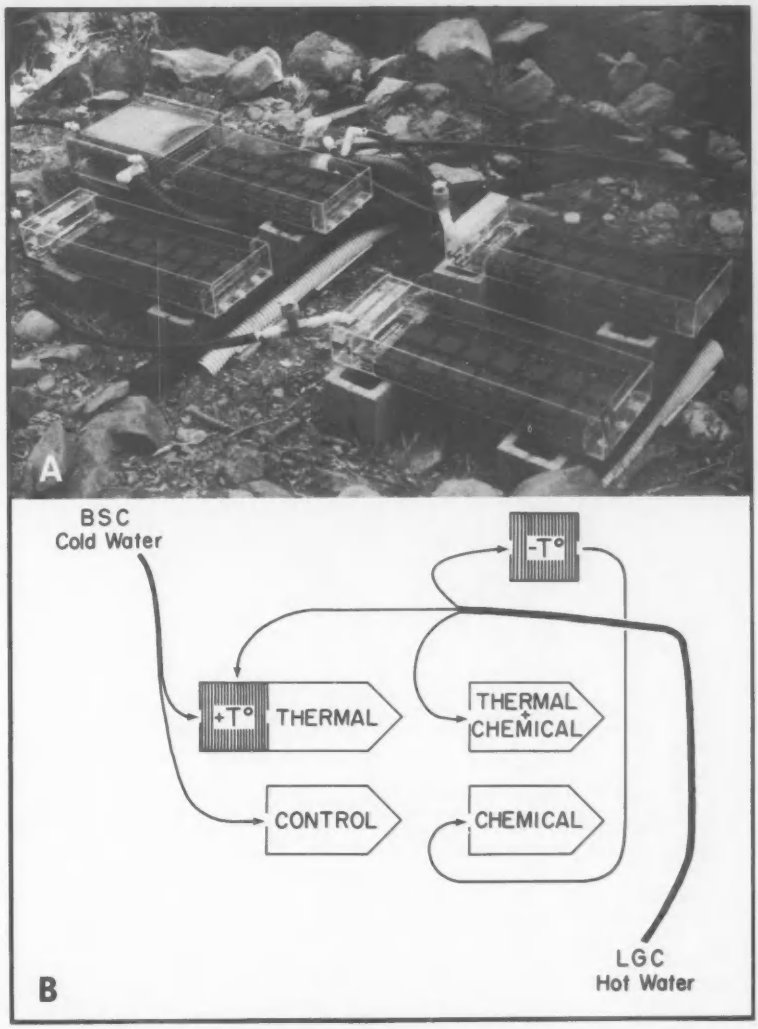

FIG. 3. Design of stream microcosm study conducted at The Geysers. (A) Photograph showing the four stream microcosms on 9 June 1981; (B) schematic diagram showing sources of water, pattern of water movement, and location of heat-exchange units (+T° in thermal microcosm and −T° in Big Sulphur Creek). Water was delivered to the microcosms solely by gravity (see text for further details). BSC, Big Sulphur Creek; LGC, Little Geysers Creek.

Sample Collection and Measurement

Tiles were leached in stream-collected water for 14 d prior to use and then scrubbed and autoclaved. After the appropriate exposure period, the tile was lifted off the substrate into a 125-μm mesh bag. Three separate 4-cm^2 scrapes of periphyton were taken from the upper surface of each tile using either a template and sterile scalpel for removing closely adherent algae (Barton and Lock 1979) or a corkborer for removing loosely attached algae (Brock 1967). One scrape was used for each of three different microbial analyses: (1) numerical abundance of bacteria, (2) amounts of chlorophyll *a* and its degradation product, phaeophytin (indices of algal standing crop), and (3) ash-free dry weight (an index of total organic content). The tile and net contents were then placed in 10% formalin, and all macroinvertebrates were later

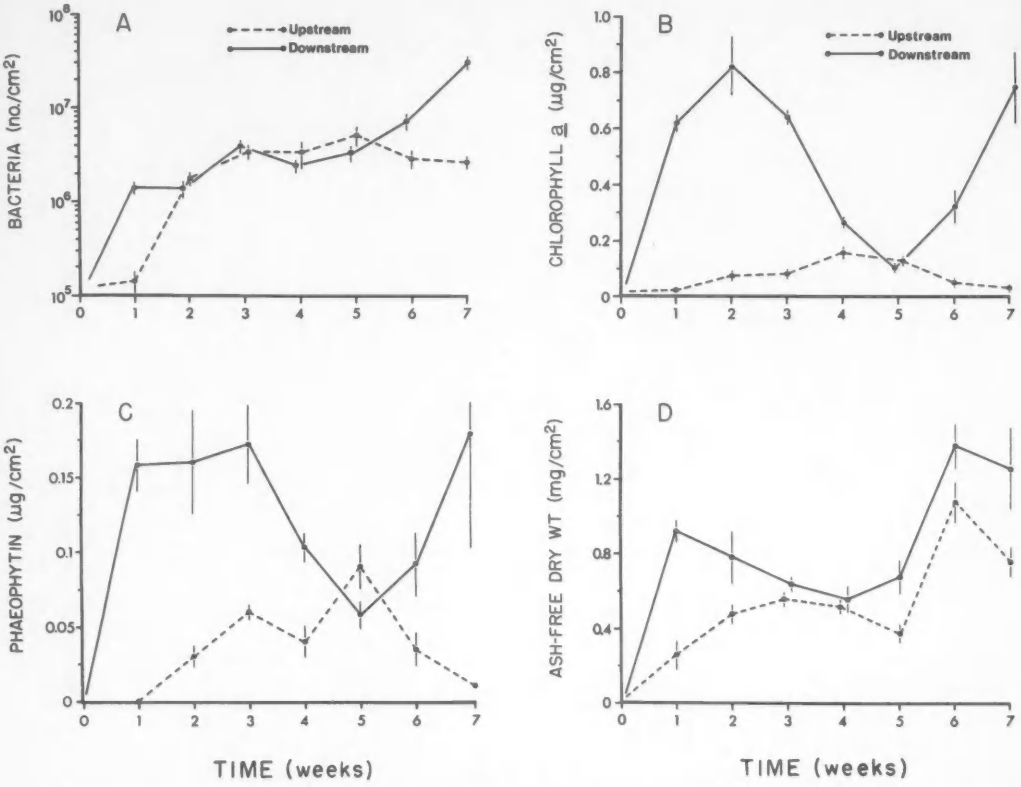

FIG. 4. Dynamics of benthic microbial components during the 7 wk (1 June – 18 July 1979) of the in-stream study that compared communities in Big Sulphur Creek at upstream and downstream of a geothermal tributary. (A) Numerical abundance of bacteria; (B) chlorophyll *a*; (C) phaeophytin; (D) total organic matter. Data points and bars represent $\bar{x} \pm$ SE ($N = 5$).

sorted, identified, and counted.

Bacteria were enumerated using epifluorescence microscopy and the acridine orange direct count (AODC) method (Hobbie et al. 1977; Barton and Lock 1979). Samples for bacterial analysis were preserved in 0.5% glutaraldehyde that was buffered with a 0.067 mol/L cacodylate solution. In the laboratory, bacteria were dispersed by blending each sample for 30 s with a Brinkman Polytron homogenizer (Barton and Lock 1979). A subsample of the homogenate was then filtered through a 0.2-µm Nuclepore membrane, stained with acridine orange, and viewed at 1500× using epifluorescence microscopy. Bacteria that fluoresced orange or green were directly counted in ten 0.016-mm² fields per membrane, and mean counts were converted into density estimates.

Samples for chlorophyll *a* and phaeophytin analyses were filtered through glass fiber filters (Whatman GF/C), fixed with $MgCO_3$, and frozen in the field. In the laboratory, the filters were homogenized and photosynthetic pigments were extracted in 90% acetone for 24 h at −10°C. Spectrophotometric absorbances of the extracts were measured and pigment concentrations were calculated for both chlorophyll *a* and phaeophytin (Moss 1967a, 1967b).

Samples for measurement of the total organic content of attached material were also filtered through glass fiber filters and frozen in the field. In the laboratory, the filters were dried (105°C) for 24 h in a vacuum oven and then ashed (500°C) for 1 h in a muffle furnace. The difference between the ash and dry weights represents the organic content (i.e. the ash-free dry weight).

All macroinvertebrates (>125 µm in size) from each tile or natural substrate sample were identified and counted. Dry weight and ash-free dry weight of formalin-preserved macroinvertebrates were obtained using the procedure outlined above for total organic content.

Differences in microbial abundances were statistically analyzed at the end of the respective study periods using Student's *t*-test. Differences in macroinvertebrate abundances were analyzed using chi-square (χ^2) tests (one-way classification), since those quantities were generally either pooled samples (in-stream study) or inventories (stream microcosms). The exception was macroinvertebrate density in the in-stream study, which was analyzed with Student's *t*-test.

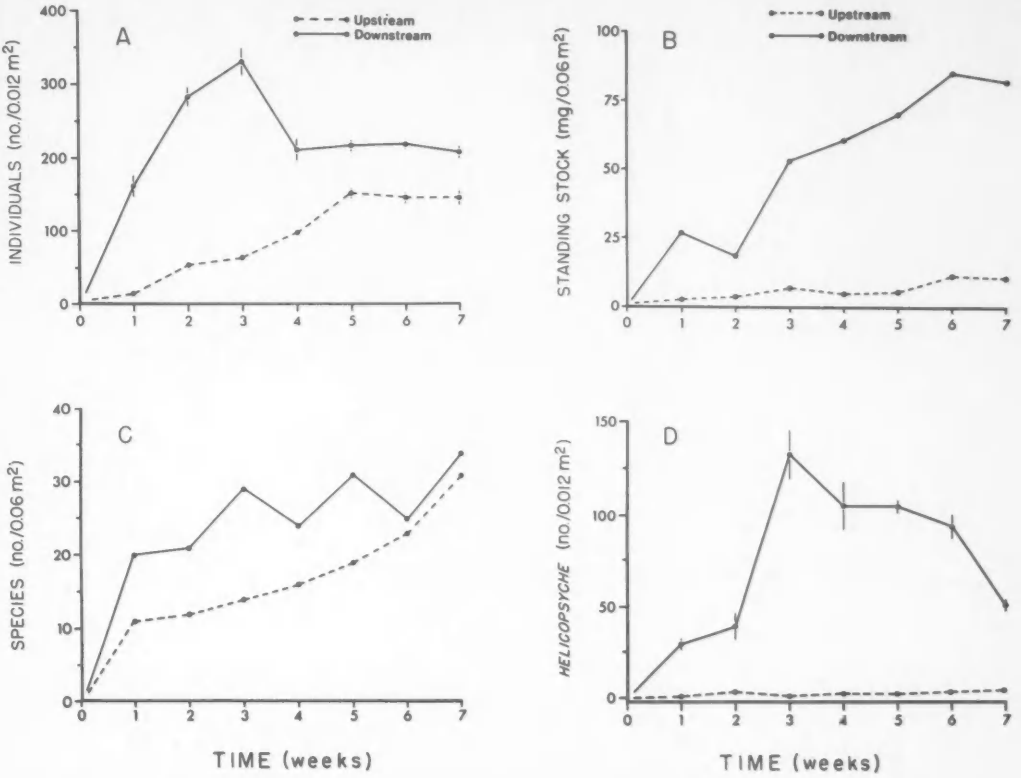

FIG. 5. Dynamics of benthic macroinvertebrates during the 7 wk (1 June − 18 July 1979) of the in-stream study that compared communities in Big Sulphur Creek at upstream and downstream of a geothermal tributary. (A) Density of all macroinvertebrates; (B) standing stock (0.06 m^2 = five samples pooled); (C) species richness (five samples pooled); (D) density of *Helicopsyche borealis* (Hagen).

Results

IN-STREAM STUDY

Our descriptive in-stream study documented the development of the microbial and macroinvertebrate communities on tiles placed in Big Sulphur Creek (BSC) at two sites: 100 m upstream (BSC-upstream) and 50 m downstream (BSC-downstream) of its geothermal tributary, Little Geysers Creek (LGC) (Fig. 1C), during the period 1 June − 18 July 1979. The biota collected from these tiles closely represented the phyto- and zoo-benthic communities that occurred on natural stream rocks (G. A. Lamberti, unpublished data).

Average water temperatures at midday during the study period were 19°C at BSC-upstream, 26.5°C at BSC-downstream, and 36.5°C in LGC. Thus, the 7.5° difference between BSC-upstream and BSC-downstream is the amount that BSC water was heated by the geothermal LGC water. In contrast, the 10° difference between LGC and BSC-downstream can be considered to be the amount that LGC water was cooled by mixing with BSC water. As previously noted, LGC also raised the concentrations of several chemical substances at BSC-downstream (Fig. 2).

Abundances of microorganisms — The density of benthic bacteria at 1 wk was about 10^6 cells/cm^2 at BSC-downstream compared with 10^5 cells/cm^2 at BSC-upstream (Fig. 4A); densities then converged and remained similar at the two sites during the middle of the study period (i.e. 2−5 wk). However, densities diverged again, and at 7 wk, there were significantly higher numbers of bacteria downstream of the geothermal input (about 10^7 cells/cm^2) than upstream (about 10^6 cells/cm^2) ($P < 0.01$).

Chlorophyll *a* remained low at BSC-upstream (<0.2 μg/cm^2) throughout the study period (Fig. 4B). At BSC-downstream, chlorophyll *a* increased to 0.8 μg/cm^2 at 2 wk, but then declined to less than 0.2 μg/cm^2 at 5 wk. Similar to the bacterial pattern at BSC-downstream, chlorophyll *a* increased again, and at 6 wk, resumed its previous high level. These fluctuations in BSC-downstream abundances were probably due to grazing by insect herbivores (see comments on macroinvertebrates below). At 7 wk,

chlorophyll *a* was significantly higher downstream of the geothermal input ($P < 0.01$).

Phaeophytin, the chlorophyll *a* degradation product, ranged from 20 to 43% of the total pigment at BSC-upstream and from 15 to 33% of total pigment at BSC-downstream and fluctuated in a manner similar to chlorophyll *a* (compare Fig. 4C, 4B). In general, there were higher amounts of phaeophytin at BSC-downstream, and at 7 wk, phaeophytin was more abundant at the downstream site than at the upstream site ($P = 0.06$).

The total organic content is a measure of microbial biomass plus associated nonliving organic material, such as fine detritus that is trapped in the microbial matrix. The total amount of benthic organic matter (i.e. ash-free dry weight) was higher at BSC-downstream throughout the study period (Fig. 4D), although the relative differences were smaller than with either chlorophyll *a* or phaeophytin (Fig. 4B, 4C). Similar to the chlorophyll *a* and phaeophytin patterns, the total organic matter at BSC-downstream displayed an initial rapid increase, followed by a decline, and then a second increase (Fig. 4D). At 7 wk, the mean organic content of the benthic material was 1.26 mg/cm^2 downstream of the geothermal input compared with 0.76 mg/cm^2 upstream ($P = 0.07$).

Abundances of macroinvertebrates — The density of macroinvertebrates (Fig. 5A) increased rapidly at BSC-downstream, peaked in 3 wk at 325 individuals/0.012-m^2 tile (27 083/m^2), and then declined and stabilized at about 200 individuals/0.012-m^2 tile (16 667/m^2). At BSC-upstream, macroinvertebrate density both peaked and stabilized in 5 wk at about 150 individuals/0.012 m^2 (12 500/m^2). At 7 wk, densities were significantly higher at BSC-downstream than at BSC-upstream ($P < 0.01$). At both sites, stable densities were reached in 5 wk, a period of time consistent with the results of many other artificial substrate colonization studies (see review by Rosenberg and Resh 1982).

The standing stock of macroinvertebrates at BSC-downstream (Fig. 5B) peaked in 6 wk at 85 mg/0.06 m^2 (1.42 g/m^2). In contrast, the standing stock at BSC-upstream remained lower than 11 mg/0.06 m^2 (0.18 g/m^2) throughout the study period. This intersite difference in standing stock was much more striking than the difference in the density of macroinvertebrates (compare Fig. 5B, 5A) and may have occurred for two reasons: (1) individuals grew at a faster rate at BSC-downstream, resulting in differences in the age structure of the populations at the two sites, or (2) there were significant differences between the two sites in the species composition of macroinvertebrates. Although we did not analyze the first alternative, accelerated growth rates of macroinvertebrates have been observed in other studies of thermal enrichment (e.g. Humpesch 1978; Laybourn 1979) and may have accounted in part for the intersite differences in standing stock in our study.

The second alternative can be assessed by examining the species richness and community structure of macroinvertebrates. The total number of macroinvertebrate species was consistently higher at BSC-downstream (Fig. 5C), although the magnitude of this difference declined near the end of the study period. At 7 wk, 34 species were collected at BSC-downstream and 31 species were found at BSC-upstream. A

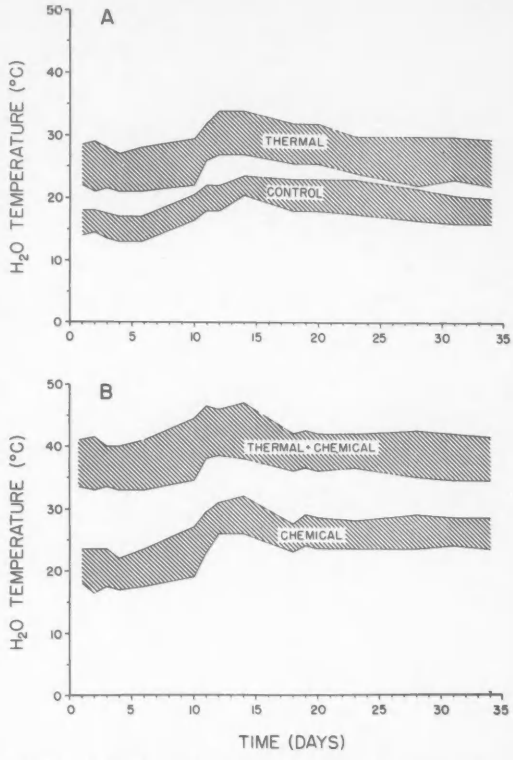

FIG. 6. Comparison of daily maximum−minimum temperature ranges in (A) control and thermal microcosms and (B) T + C and chemical microcosms during the 34-d study period (9 June − 13 July 1981).

combined total of 53 species were collected at the two sites during the 7-wk study; of these, 33 species (62%) occurred at both sites. Thus, although most species were found at both sites, there were some differences in the composition of the macroinvertebrate communities. This was especially true for the insect component of the macroinvertebrate fauna. For example, six species of Odonata were found at BSC-downstream, but only two species occurred at BSC-upstream. Three species of stoneflies (Plecoptera) were collected at BSC-downstream, but none were found at BSC-upstream.

Although some aquatic insect orders showed similar species richness at the two sites, the component populations frequently differed in their densities. For example, we collected 9 species of Trichoptera at BSC-upstream and 10 species at BSC-downstream, of which 8 species were found at both sites. However, *Helicopsyche borealis* (Hagen), which is a highly thermotolerant caddisfly frequently found in thermally enriched habitats (Wiggins 1977; Mackay and Wiggins 1979), occurred in much higher densities at the geothermally enriched downstream site (Fig. 5D). *Helicopsyche* larvae graze algae in BSC and probably accounted for the fluctu-

TABLE 1. Dissolved oxygen concentration, conductivity, and pH in each stream microcosm ($\bar{x} \pm$ SD). Statistical comparisons were made with Student's *t*-test; NS = no significant difference.

	Control	Thermal	*P*	Chemical	Thermal + chemical	*P*
O_2 (mg/L)	7.6±0.6 (N = 11)	6.8±0.6 (N = 11)	<0.01	4.6±0.2 (N = 11)	4.2±0.2 (N = 11)	<0.01
µS/cm	340±65 (N = 11)	400±70 (N = 11)	0.05	370±25 (N = 11)	560±30 (N = 11)	<0.01
pH	7.2±0.4 (N = 8)	7.2±0.3 (N = 8)	NS	6.6±0.2 (N = 8)	6.7±0.2 (N = 8)	NS

ations in chlorophyll *a* at BSC-downstream (compare Fig. 4B, 5D; see also Lamberti and Resh 1983). Brock (1967) suggested that other grazing macroinvertebrates may play a similar role in thermal streams of Yellowstone National Park at temperatures less than 50°C.

STREAM MICROCOSM STUDY

We used the stream microcosms (Fig. 3A) to analyze separately the thermal and chemical components of the geothermal fluids. This experiment was designed to last 5 wk, since the results of the in-stream study indicated that the density of macroinvertebrates stabilized in 4–5 wk (Fig. 5A). In the in-stream study, the abundances of microorganisms continued to fluctuate past this point (Fig. 4), but because of the continued grazing by macroinvertebrates, those abundances may never have completely stabilized.

Macroinvertebrates and microorganisms colonized the four microcosms primarily by their drift in water carried through the system's inflow pipes (Fig. 3B). Although the tops of the microcosms were left open (to ensure normal light regimes), oviposition was probably a minor component of the colonization process compared with drift (e.g. only one egg mass, that of a Trichopteran, was observed in the microcosms), and there was no evidence of colonization by flying adults (e.g. no adult Coleoptera of the families Dytiscidae or Hydrophilidae were collected). Because of the different sources of colonists, the valid comparisons in this experiment were (1) between the control and the thermal microcosms, whose common source of colonists was drift from BSC-upstream, and (2) between the T + C and chemical microcosms, whose common source of colonists was drift from LGC.

The design of the heat-exchange elements of the microcosms resulted in effective heating of nongeothermal water (Fig. 6A) and effective cooling of geothermal water (Fig. 6B). To determine the average temperature difference between the two microcosms of each comparison, we first calculated the midpoint of each daily maximum–minimum reading and then the mean difference between midpoints for the entire 34-d experimental period. Thus, cool BSC-upstream (i.e. control) water was heated an average of 8.5° in the thermal microcosm, an increase very close to the natural heating (7.5°) of BSC by the inflow of LGC that was observed in the in-stream study. Hot LGC (i.e. T + C) water was cooled an average of 14.5° before it entered the chemical microcosm, a reduction somewhat larger than the natural cooling (10°) of LGC by mixing with BSC. However, this further cooling of LGC water was advantageous because it allowed greater isolation of chemical from temperature effects. Water temperatures in all four microcosms increased during days 5–15 (Fig. 6), coinciding with a gradual rise in air temperature.

As described for the in-stream study, certain chemical substances were carried in much higher concentrations in LGC water than in BSC-upstream water (Fig. 2). Since these increases were measured at BSC-downstream (following about a 3:1 dilution of LGC water by BSC-upstream water), these differences indicate that those chemicals were carried in even higher concentrations in LGC, which was the direct (i.e. undiluted) water source for the T + C and chemical microcosms. In contrast, the control and thermal microcosms had the comparatively low chemical concentrations of BSC-upstream water.

The midday dissolved oxygen concentration (Table 1) was slightly lower in the warmer microcosm of each experimental pair (i.e. 0.8 mg/L difference between the control and thermal microcosms and 0.4 mg/L difference between the chemical and T + C microcosms). Since conductivity is positively influenced by temperature, it was slightly higher in the warmer microcosm of each experimental pair, but the absence of chemical precipitates indicated that dissolved salt concentrations were probably not altered by the temperature changes. The pH was always near neutral in all four microcosms.

Responses of microorganisms — Bacteria grew rapidly in all four microcosms during the period 0–20 d (Fig. 7A, 7B); bacterial density stabilized in the control microcosm at 20 d but continued to increase in the other microcosms. At 34 d, the density of benthic bacteria was significantly higher in the thermal microcosm than in the control microcosm (Fig. 7A, $P < 0.01$). However, there was no significant difference in bacterial density between the chemical and T + C microcosms (Fig. 7B, $P = 0.45$). Thus, the addition of a thermal component to the control water apparently encouraged bacterial growth, but removal of the thermal component from the T + C water had little effect on bacterial density.

The species composition and standing crop of algae both showed striking differences among the microcosms. Algae in the control microcosm consisted principally of a thin layer of diatoms (Chrysophyta: Bacillariophyceae) but also included small amounts of the filamentous green alga *Spirogyra* (Chlorophyta: Zygnemataceae); in the thermal microcosm, *Spirogyra* predominated and grew into a thick mat that covered the substrate. Under the extreme temperature and chemical conditions in the T + C microcosm, thermophilic blue-green algae (Cyanophyta) predominated, with *Oscillatoria*, a

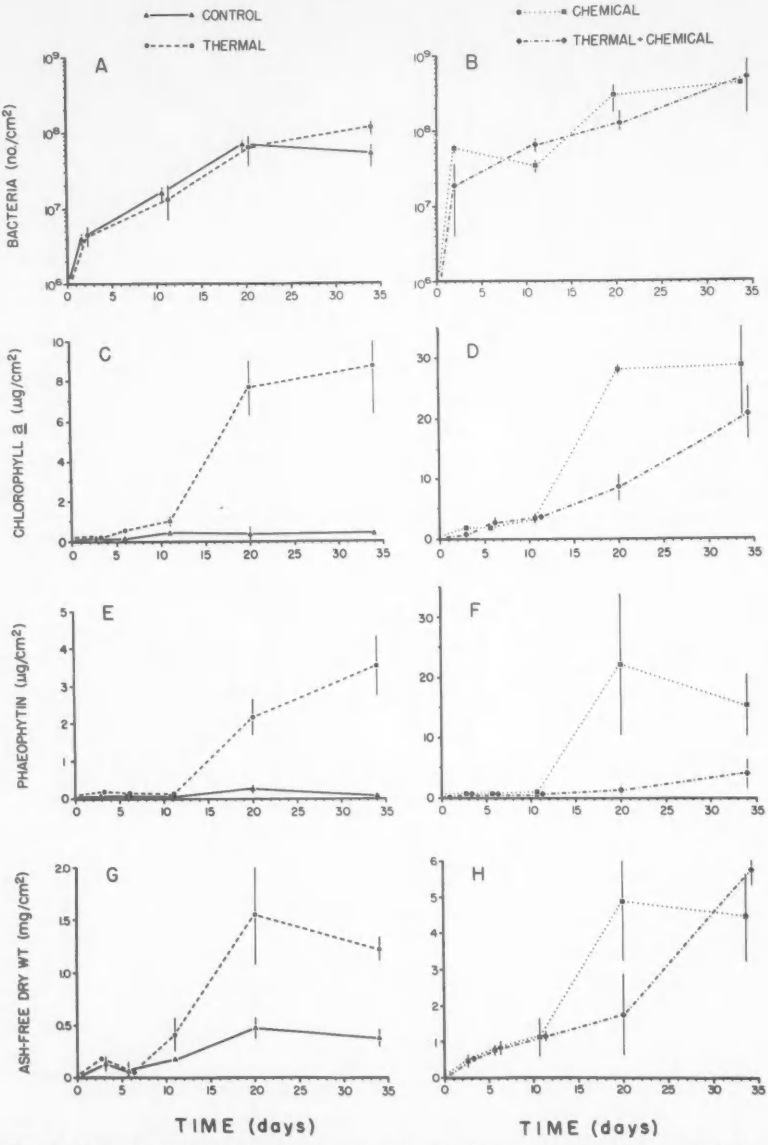

FIG. 7. Dynamics of benthic microbial components in each of the four stream microcosms during the 34-d study period (9 June – 13 July 1981). (A, B) Numerical abundance of bacteria; (C, D) chlorophyll *a*; (E, F) phaeophytin; (G, H) total organic matter. Data points and bars represent $\bar{x} \pm 95\%$ confidence interval ($N = 3$).

filamentous blue-green, and *Aphanocapsa*, a colonial unicellular form, being the numerically dominant taxa. In the chemical microcosm, there was a mixture of green and blue-green algae, with *Spirogyra* and *Oscillatoria* being numerically dominant.

Algal standing crop (as indicated by chlorophyll *a* and phaeophytin) increased slowly from 0 to 10 d in all four microcosms (Fig. 7C–7F). In the thermal and chemical microcosms, algal growth accelerated at 10 d but then stabilized at 20 d. Algal biomass remained low in the control

TABLE 2. Export of periphyton from each stream microcosm. Export is mean dry weight collected during five separate 24-h periods. Standing crop is mean dry wt/cm^2 at the end of the 34-d study period, extrapolated to the entire microcosm (0.22 m^2).

	Control	Thermal	Chemical	Thermal + chemical
Export (g/d)	0	0.16	0.15	0.81
Standing crop (g/0.22 m^2)	10.33	16.51	27.98	37.26
Export/d (% standing crop)	0	0.97	0.54	2.17

microcosm throughout the study period but increased steadily in the T + C microcosm. Both chlorophyll *a* and phaeophytin were significantly higher in the thermal microcosm than in the control at 34 d (Fig. 7C, $P < 0.01$; Fig. 7E, $P < 0.01$). In the other comparison, chlorophyll *a* and phaeophytin were lower in the T + C microcosm than in the chemical microcosm at 34 d (Fig. 7D, $P = 0.06$; Fig. 7F, $P < 0.01$).

The amount of chlorophyll *a* degraded into phaeophytin provides some indication of the physiological state of the algae, because the relative abundance of phaeophytin frequently increases with declining algal productivity (Vollenweider 1969). Since the average degradation proportions at 34 d were similar in the thermal (29%) and control (24%) microcosms, algae were apparently of comparable vigor in these two microcosms. In contrast, phaeophytin occurred in higher proportions in the chemical (34%) than in the T + C (14%) microcosm at 34 d. Thus, although chlorophyll *a* and phaeophytin were more abundant in the chemical microcosm than in the T + C, the algae in the T + C microcosm were probably in a better physiological state.

These differences in proportions may be related to the relative productivity (i.e. rate of tissue elaboration) of algae in the T + C and chemical microcosms. Blue-green algae grew in a loosely attached mat on the substrate of the T + C microcosm, a growth form frequently seen in other thermal habitats as well (Brock 1978). We observed that portions of this mat periodically lifted off the substrate, tore free from the remainder of the mat, and drifted out of the microcosm; this bare area was then rapidly covered by new growth. Thus, this sloughed algae represented primary production that was not expressed in the standing crop figures. The measurable export of algae per unit time is referred to as the "washout rate" by Brock (1970). We measured the algae exported from each microcosm during five separate 24-h periods by collecting the sloughed algae in 1.0-mm mesh nets placed directly under the outflows. There was no measurable export of algae from the control microcosm (Table 2). Similar amounts of algae were exported from the thermal and the chemical microcosms (about 0.15 $g \cdot 0.22\ m^{-2} \cdot d^{-1}$). When compared with the standing crops of periphyton, these represented daily exports of about 1% of the total standing crop from the thermal microcosm and 0.5% from the chemical microcosm. Export from the T + C microcosm (0.81 $g \cdot 0.22\ m^{-2} \cdot d^{-1}$) was much higher than from the other microcosms and represented a daily export of more than 2% of the total microbial biomass.

Although the standing crop of algae was slightly higher in the chemical microcosm than in the T + C microcosm (Fig. 7D), algal production was probably higher in the T + C microcosm, since the standing crop of blue-green algae was periodically reduced by sloughing. The low proportion of algal phaeophytin (14%) in the T + C microcosm further substantiates the observed pattern of sloughing and vigorous regrowth that distinguished the thermophilic algae of this microcosm from those of the other three microcosms. The estimated export rates probably represented a slight underestimate of actual export, since the catchment nets did not retain algal clumps less than 1.0 mm in diameter. However, because most algae were sloughed in relatively large (>1.0 mm in diameter) patches, this underestimate was probably small.

The total amount of organic matter in the thermal microcosm was higher than in the control microcosm at all times after 6 d (Fig. 7G, $P < 0.01$), as would be suggested by the abundances of its microbial components (e.g. bacteria, chlorophyll *a*). However, unlike the algal components considered alone, the total organic matter was slightly higher in the T + C microcosm than in the chemical microcosm (Fig. 7H, $P = 0.03$).

Responses of macroinvertebrates — We inventoried the entire macroinvertebrate fauna of each microcosm at 34 d. The thermal microcosm had about 25% fewer individuals than the control microcosm (Fig. 8A, $P < 0.01$). However, there was no difference in the standing stock of macroinvertebrates in those two microcosms (Fig. 8B). As previously hypothesized for the in-stream study, this may have been due to accelerated growth rates of macroinvertebrates in the thermally enriched habitat.

Macroinvertebrate species richness was similar in the control and thermal microcosms (45 and 44 species, respectively) (Fig. 8C), as was species composition. For example, a combined total of 54 species were found in the two microcosms, of which 35 species were shared by the microcosms (65%); these totals are very similar to those found in the in-stream study (i.e. 53 total; 33 shared between sites). Apparently, most species from the cool section of BSC that colonized the control microcosm were also able to tolerate the 8.5° increase in water temperature in the thermal microcosm. However, some differences did exist. For example, the caddisflies *Rhyacophila* and *Lepidostoma*, which are taxa that normally occur in cool, well-oxygenated streams (Wiggins 1977), were found in the control but not in the thermal microcosm.

The distribution of those 54 species among the insect orders and other groups showed broad taxonomic diversity. There were 18 species of Diptera (33% of total), nine species of Coleoptera (17%), eight species of Trichoptera (15%), seven species of Ephemeroptera (13%), three species of Plecoptera (6%), and one species each of Odonata, Megaloptera, and Hemiptera. Noninsect taxa (e.g. crustaceans and oligochaetes) included six species (11% of total).

Macroinvertebrates were virtually absent from the T + C microcosm (Fig. 8A, 8B). Only 85 individuals and three species were found in this microcosm, including 66 larvae (78% of total) of the chironomid midge *Tanytarsus*. The remaining macroinvertebrates were an oligochaete species (11%) and the ceratopogonid fly larva *Palpomyia* (11%). Accordingly, the standing crop of macroinvertebrates was low in the T + C

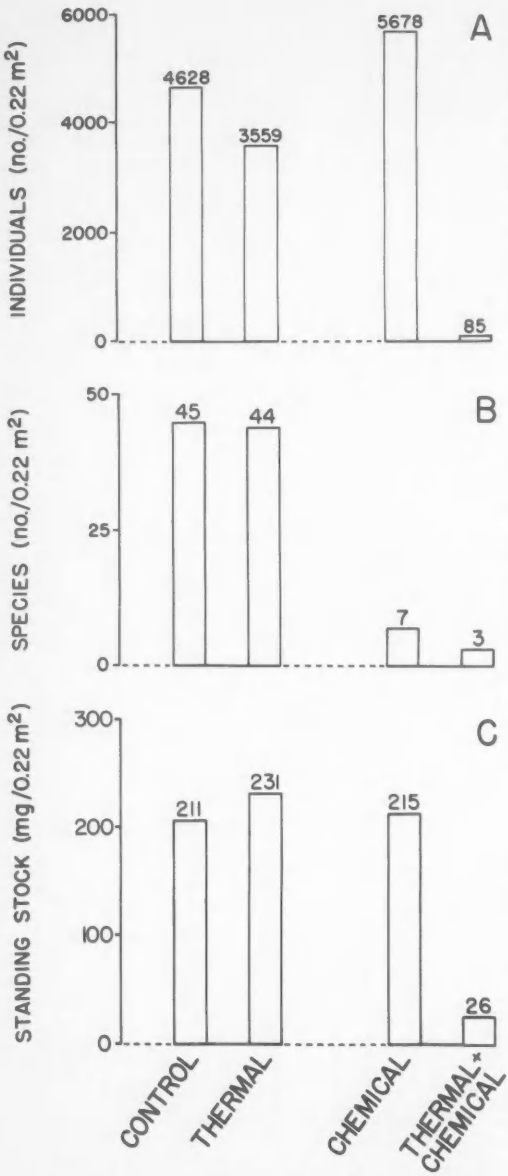

FIG. 8. Inventory of benthic macroinvertebrates in each of the four stream microcosms at the end of the 34-d study period (13 July 1981). (A) Density of all macroinvertebrates; (B) species richness; (C) standing stock (dry weight).

microcosm (Fig. 8C).

Macroinvertebrates reached the highest density in the chemical microcosm (Fig. 8A), where water temperature was reduced from that found in the extreme T + C microcosm (i.e. maximum temperature of 32 vs 47°C) (Fig. 6B). Standing stock in the chemical microcosm was also much greater than in the T + C microcosm (Fig. 8B, $P < 0.01$). Similar to the T + C microcosm, species richness in the chemical microcosm was low (i.e. seven species) (Fig. 8C). Diversity was inherently restricted in both microcosms because colonists came from the geothermal LGC. However, those species that colonized the chemical microcosm, when released from the extreme thermal stress, reached high densities. In the chemical microcosm, as in the T + C, *Tanytarsus* was the most abundant macroinvertebrate (52% of total). Other abundant species in the chemical microcosm were the chironomid midge *Polypedilum* (14%) and an oligochaete (26%). The results of both the stream microcosm experiment and the in-stream study are summarized in Table 3.

Discussion

The stream microcosm study was not designed to simultaneously compare a control to three treatments (i.e. thermal, chemical, and T + C); instead, two separate controlled experiments were conducted. In one experiment (i.e. comparison of T + C and chemical), the thermal component was removed from geothermal water. In the other (i.e. comparison of control and thermal), a thermal component was added to nongeothermal water.

In the T + C−chemical comparison, removal of the thermal component from geothermal water resulted in an algal community with higher standing crop but lower productivity, and a macroinvertebrate community with a higher density and standing crop. Therefore, many macroinvertebrates could tolerate the chemical conditions of geothermal water, but combined chemical and extreme thermal stresses eliminated most macroinvertebrates.

In the control−thermal comparison, thermal enrichment of nongeothermal water had dramatic effects on the benthic microbial community. The abundance of benthic chlorophyll *a* was increased 40 times by solely increasing the temperature by 8.5° (i.e. thermal microcosm). Likewise, algal productivity, as indicated by the export rate, was markedly accelerated, and the density of benthic bacteria increased 2 times. These patterns of relative increase are strikingly similar to those observed in the in-stream study, in which chlorophyll *a* was also about 40 times higher at the downstream site (i.e. +7.5° and geochemicals) after 7 wk, and bacterial density also moderately increased. Apparently, thermal enrichment alone of BSC water (thermal microcosm) enhanced microbial growth in nearly the same proportions as thermal and chemical enrichment combined (BSC-downstream). The generally lower absolute amounts of algae and bacteria found in the in-stream study compared with those of the microcosms (e.g. compare Fig. 4B, 7C) were probably related to the grazing effects of herbivorous insects in BSC. For example, since the dominant grazer *Helicopsyche borealis* displays a very low tendency to drift (Lamberti and Resh 1983) and thus failed to colonize the microcosms, it could not depress microbial standing crop in the microcosms.

Less dramatic responses to thermal enrichment were observed among benthic macroinvertebrates; their density was only about 25% lower in the thermal microcosm than in the

TABLE 3. Summary of statistical comparisons of microbial and macroinvertebrate abundances for the in-stream study and the stream microcosm study at the end of the respective study periods. I = increase in first habitat of listed pair; D = decrease; NC = no change; [a]$P < 0.01$; [b]$P < 0.05$; [c]$P < 0.10$.

	In-stream study	Stream microcosms	
	BSC-downstream vs BSC-upstream	Thermal vs control	Chemical vs T + C
Microorganisms			
Bacteria	I[a]	I[a]	NC
Chlorophyll *a*	I[a]	I[a]	I[c]
Phaeophytin	I[c]	I[a]	I[a]
Ash-free dry wt	I[c]	I[a]	D[b]
Macroinvertebrates			
Density	I[a]	D[a]	I[a]
Standing stock	I[a]	NC	I[a]
Species richness	NC	NC	NC

control microcosm, and standing stock and species richness were nearly the same in both microcosms. These results appear to contradict the findings of the in-stream study, in which macroinvertebrate density and biomass were markedly higher at the geothermally influenced downstream site. We would expect this higher abundance of macroinvertebrates at BSC-downstream because its colonists came from both the geothermal LGC and the nongeothermal upstream section of BSC (Fig. 1C), and thus they probably represented a broad range of thermal tolerances. We would not, however, expect the density to increase in the thermal microcosm because its colonists came only from BSC-upstream (Fig. 3B), and thus they probably represented a narrow range of thermal tolerances. The substantial number of species shared by the control and thermal microcosms does confirm, though, that many of the macroinvertebrates from BSC-upstream could tolerate a moderate increase in water temperature.

Brock (1975) postulated that the microbiota of aquatic habitats with temperatures below 25°C should be more severely affected by thermal enrichment than the biota of habitats with naturally higher temperatures. This is because few microorganisms have growth optima at temperatures less than 25°C. Consequently, when cool-water habitats are warmed above 25°C, the growth rates of certain microorganisms should accelerate, thereby leading primarily to increases in total microbial production and secondarily to changes in community structure. In the stream microcosm study, the primary pattern was illustrated by *Spirogyra*, which had a much higher standing crop in the heated thermal microcosm (T_{max} = 34°C) than in the control microcosm (T_{max} = 23°C). In contrast, habitats with natural temperatures above about 25°C should have at least some species growing optimally. Further temperature increases should primarily result in changes in community structure rather than in standing crop, because some of those species will be replaced by different optimally growing species. In our study, the mixture of green and blue-green algae in the chemical microcosm (T_{max} = 32°C) was replaced by solely blue-green algae in the T + C microcosm (T_{max} = 47°C) but without significant increases in standing crop. Wilde and Tilly (1981) recorded similar shifts to blue-green dominance in thermally enriched ($T_{max} > 30$°C) microcosms.

Thermal discharges have complex effects on macroinvertebrate communities that may vary on both temporal and spatial scales (Ward and Stanford 1982). For example, increased water temperature may either advance (Fey 1977) or delay (Wise 1980) the emergences of aquatic insects. In some instances, thermal enrichment may significantly reduce species richness (e.g. Logan and Maurer 1975; Dusoge and Wiśniewski 1976; Ferguson and Fox 1978). In other instances, certain macroinvertebrate taxa may respond positively, in both density and standing stock, to thermal additions. For example, thermal enrichment frequently increases the relative abundance of oligochaetes (e.g. Nichols 1981; Rasmussen 1982) and chironomid midges (e.g. Vincent 1967; Ferguson and Fox 1978; Rasmussen 1982). Previous studies of geothermal inputs into natural systems have shown little reduction in macroinvertebrate species richness, although there may be shifts in species composition (Armitage 1958; Vincent 1967), findings that are similar to the results of our in-stream study. However, at extreme geothermal conditions, such as in the T + C microcosm, most macroinvertebrate species are eliminated and the community is dominated by chironomids and oligochaetes.

In many cases, thermal enrichment accelerates the growth rates of aquatic invertebrates, as documented in groups ranging from the Ephemeroptera of the Insecta (Humpesch 1978; Mattice and Dye 1978) to the Oligochaeta (Wiśniewski 1976), the Nematoda (Laybourn 1979), and the Copepoda (Geiling and Campbell 1972). In both our in-stream and microcosm studies, accelerated growth rates of some macroinvertebrate populations may have contributed to the increased standing stock in the thermally enriched habitats. Our nonexperimental in-stream study demonstrated that a moderate addition of geothermal fluids into a nongeothermal stream could substantially alter the structure of the benthic community. However, our in-stream analysis did not establish the cause of the alteration. In contrast, our experimental stream microcosm study demonstrated that the thermal component of those geothermal fluids had greater influence than the chemical component in determining the structure of the benthic community in Big Sulphur Creek.

The development of in situ (i.e. field-based) bioassay procedures can greatly extend our knowledge of the effects of chemicals and water temperature on aquatic biota (Alabaster 1978; Little and Maciorowski 1979). Such experimental approaches may be particularly effective for predicting the principal effects of environmental disturbances, once the main impacting factors have been identified (Rosenberg et al. 1981). Laboratory bioassay tests of chemical toxicity (LC50) or thermal tolerance (LT50) often have limited relevance to conditions in natural systems (Brock 1975), especially if conducted as short-term (i.e. acute) shock tests (Lehmkuhl 1979). Specific criticisms of such procedures have centered on (1) concentration of test chemical, (2) duration of test, (3) trophic level and source of test organisms, (4) use of a single chemical as opposed to naturally occurring mixtures, (5) selection of temperature, (6) lack of environmental variation imposed by field conditions, and (7) failure to assess broad taxonomic groups (Gray and Ventilla 1973).

In contrast, a well-designed in situ bioassay can vary

important physical–chemical features while allowing natural environmental variation to exert some influence over the bioassay. For example, our stream microcosm study accomplished this goal and answered the above criticisms by (1) exposing benthic communities to chemical concentrations typically found in geothermal habitats, (2) allowing sufficient time for biological response to occur, (3) assaying a wide range of trophic levels (autotrophs, microheterotrophs, macroheterotrophs) found in the natural community, (4) using mixtures of geochemicals that occur naturally, (5) using natural thermal regimes, (6) incorporating environmental variation encountered in the natural system, and (7) assessing the responses of many taxonomic groups, from bacteria to metazoans. In future studies designed to evaluate the environmental effects of geothermal energy development, or other sources of benthic disturbance, field-based bioassay experiments may allow cause-and-effect relationships to be more clearly elucidated than either descriptive studies or laboratory bioassays alone. Consequently, mitigation procedures can be directed to the precise cause of the benthic impact.

Acknowledgments

We thank E. McElravy and J. Wood for field assistance, A. Horne, M. Lock, and L. Volkman for valuable discussion, and S. Balling and T. D. Brock for their comments on the manuscript. Pacific Gas and Electric Company, California, provided water chemistry data. The research leading to this report was supported by the Office of Water Research and Technology, USDI, under the Annual Cooperative Program of Public Law 95-467, and by the University of California Water Resources Center, as part of Office of Water Research and Technology Project No. A-084-CAL and Water Resources Center Project UCAL-WRC-W-612.

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Effect of Somatic Growth and Reproduction on Biomass Transfer up Pelagic Food Webs as Calculated from Particle-Size-Conversion Efficiency

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BORGMANN, U. 1983. Effect of somatic growth and reproduction on biomass transfer up pelagic food webs as calculated from particle-size-conversion efficiency. Can. J. Fish. Aquat. Sci. 40: 2010–2018.

Biomass or energy transfer up pelagic food webs to larger sized organisms is a function of (1) direct trophic level transfer through predation, (2) somatic growth, a process that augments biomass transfer through predation, and (3) reproduction, which impedes biomass transfer by moving biomass down the food web to smaller sizes. By assuming that particle-size-conversion efficiency (log (food consumed/biomass produced)/log (predator–prey size ratio)) is relatively constant, I derive simple equations to calculate the effect of somatic growth and reproduction on biomass transfer up the food web. This defines the conditions under which somatic growth and reproduction can be ignored and biomass flow can be calculated from predation alone, using a previously developed model. When these conditions are not met, the effect of somatic growth and reproduction can be calculated from data on cohort growth and mortality rates. It is not necessary to identify the food of any species. This eliminates one of the problems often encountered when modeling food webs. I have applied these equations to production of *Mysis relicta*. If the estimates of *Mysis* abundance and growth rates are correct, then size-corrected production is about 25% greater for this species when somatic growth is accounted for in the calculations. This is because mortality of young *Mysis* appears to be low and most production occurs during somatic growth and not during reproduction.

BORGMANN, U. 1983. Effect of somatic growth and reproduction on biomass transfer up pelagic food webs as calculated from particle-size-conversion efficiency. Can. J. Fish. Aquat. Sci. 40: 2010–2018.

Le transfert de biomasse ou d'énergie vers le haut dans les réseaux alimentaires pélagiques dans des organismes plus gros est fonction (1) du transfert direct de niveau trophique par prédation, (2) de la croissance somatique, processus qui favorise le transfert de biomasse par prédation et (3) de la reproduction, qui retarde le transfert de biomasse en dirigeant cette dernière vers le bas dans des organismes plus petits dans le réseau alimentaire. En supposant que le rendement de conversion par taille de particules (log (nourriture consommée/biomasse produite)/log (rapport de taille prédateur–proie)) est relativement constant, j'ai pu déduire des équations simples permettant de calculer l'effet de la croissance somatique et de la reproduction sur le transfert de biomasse vers le haut dans le réseau alimentaire. Les conditions sont alors définies dans lesquelles la croissance somatique et la reproduction peuvent être négligées et le flux de biomasse calculé à partir de la prédation seule, utilisant un modèle mis au point antérieurement. Quand ces conditions sont absentes, on peut calculer l'effet de la croissance somatique et de la reproduction à partir de données sur la croissance et les taux de mortalité des cohortes. Il n'est pas nécessaire d'identifier la nourriture d'aucune espèce. Ceci permet d'éliminer un des problèmes souvent rencontré dans la modélisation des réseaux alimentaires. J'ai appliqué ces équations à la production de *Mysis relicta*. Si les estimations de l'abondance et des taux de croissance de *Mysis* sont correctes, la production corrigée pour tenir compte de la taille est d'environ 25 % plus grande pour cette espèce quand les calculs tiennent compte de la croissance somatique. C'est que la mortalité des jeunes *Mysis* semble faible et que la majeure partie de la production a lieu pendant la phase de croissance somatique et non pendant la reproduction.

Received February 11, 1983
Accepted July 29, 1983

Reçu le 11 février 1983
Accepté le 29 juillet 1983

Printed in Canada (J7243)
Imprimé au Canada (J7243)

CALCULATION of biomass or energy flow through aquatic food webs has usually been a difficult task because these ecosystems often contain many species with numerous interactions. In most cases complete information on feeding and growth rates, as well as prey selection, for all important species in an ecosystem is not available. This creates difficulties in applying typical coupled process models, and some authors have suggested that greater emphasis be placed on more holistic models (e.g. Platt et al. 1981; Kerr 1982). One such model involves the observation that logarithmically equal size-classes contain roughly similar biomasses (Sheldon et al. 1972). An explanation for this was given by Kerr (1974). Sheldon et al. (1977) applied the model to compare primary and fish production in the oceans. The analysis of Kerr (1974) dealt with discrete trophic levels, whereas Platt and Denman (1977, 1978) explained the shape of the biomass spectrum using a continuous model of biomass flow, not dependent on the trophic level concept. We have applied similar principles to derive a model of biomass flow up pelagic food webs based on the assumption of a constant particle-size-conversion efficiency (Borgmann 1982; Borgmann and Whittle 1983). Our model deals with discrete species (rather than a continuous flow up the size spectrum) but allows for any level of web complexity (not just food chains). It also differs from most other size spectrum models in that it is essentially a biomass flow model that can be adapted to predict biomass, not the other way around. It does not require any assumptions about the shape of the biomass size spectrum to estimate biomass flow (Borgmann 1982) and production can therefore be modeled with fewer assumptions. Our model is also well suited for the analysis of routine surveillance data on contaminant concentrations in aquatic organisms (Borgmann and Whittle 1983).

An important feature of aquatic food webs that is often ignored in simple models (including our model based on particle-size-conversion efficiency) is the effect of somatic growth and reproduction on biomass transfer up the food web. During somatic growth, an organism may substantially increase its size and therefore also its trophic level (e.g. Kerr 1979). This results in movement of biomass up the size spectrum without direct food chain transfer. Alternatively, large adults may feed at one trophic level but produce offspring of a small size at a lower trophic level. This causes a temporary movement of biomass down, rather than up the food web. Silvert and Platt (1980) discussed some of these problems, but their equations are complex and they did not give specific examples of how these may be applied to investigate the relative importance of somatic growth and reproduction versus predation. In the discussion below, I will demonstrate how the assumption of a constant particle-size-conversion efficiency can be applied to demonstrate the effect of somatic growth and reproduction on the efficiency of biomass transfer up the food web, thereby expanding our model to incorporate these important processes. I will show under what conditions somatic growth and reproduction can be ignored. Furthermore, the equations are written in a form that allows analysis of cohort data, such as that collected for conventional production calculations for single species. This provides a useful link between common single-species production equations and the "holistic" model. A useful feature of the model is that it is not necessary to identify who feeds on what, while still permitting estimation of biomass flow through the food web.

Theory

A THREE-SPECIES FOOD CHAIN

Particle-size-conversion efficiency (ϵ) and its application to calculation of pelagic production for ecosystems where all species have relatively uniform body sizes has been discussed by Borgmann (1982). Particle-size-conversion efficiency was defined as

$$(1) \quad \epsilon = \frac{\log (C_j/P_j)}{\log (W_j/W_i)}$$

which gives

$$(2) \quad \frac{P_j}{C_j} = K_1 = \left(\frac{W_i}{W_j}\right)^{\epsilon}$$

where C_j is the food consumed by a predator, P_j is the biomass produced by the predator, and W_j and W_i are the body size of the predator and its prey, respectively (the subscripts have been simplified from Borgmann (1982) because equation 1 here refers to a food chain rather than a food web). K_1 is the conventional definition of conversion efficiency, and ϵ is a measure of the efficiency with which biomass is transferred from one size to a larger size organism rather than from one trophic level to another. Several authors have suggested that conventional conversion efficiency (K_1) increases with increasing prey size, relative to predator size (e.g. Paloheimo and Dickie 1966; Kerr 1971), suggesting that ϵ may be relatively constant. Borgmann (1982) showed that ϵ varied slightly less than log K_1 for published data on invertebrate predators and suggested that it was at least as valid to assume a constant ϵ when modeling a food chain as it is to assume a constant K_1.

The advantage of applying the particle-size-conversion efficiency concept to ecosystem modeling is shown below, using a three-species food chain with species having body size W_1, W_2, and W_3 (Fig. 1A). Applying equation 2, and assuming that all production at one trophic level is consumed by the next trophic level (i.e. $P_1 = C_2$, $P_2 = C_3$, etc.), gives

$$(3) \quad W_3^{\epsilon}P_3 = W_2^{\epsilon}C_3 = W_2^{\epsilon}P_2 = W_1^{\epsilon}C_2 = W_1^{\epsilon}P_1.$$

This can be rewritten as

$$(4) \quad P_3^* = P_2^* = P_1^* = F, \qquad P_i^* = W_i^{\epsilon}P_i$$

where F is the flow of size-corrected biomass through the food chain (Borgmann 1982). Here, production on a size-corrected basis (i.e. multiplied by W_i^{ϵ}) is shown to be equal at all trophic levels and P_3^* can therefore be calculated from P_1^* without any knowledge of P_2 or W_2 as long as ϵ is relatively constant. Application of equation 4 has permitted us to estimate potential fish production in Lake Ontario from data on zooplankton production (Borgmann and Whittle 1983). However, the above equations do not allow for changes in body size as organisms grow from newly hatched to adult sizes, a process

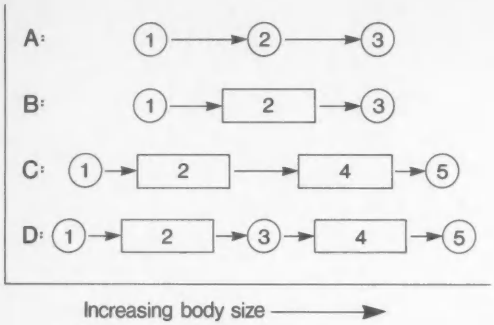

FIG. 1. Four hypothetical food chains. Circles represent species in which all individuals are of one constant size. Rectangles represent species in which individual size varies due to periods of somatic growth alternating with periods of reproduction.

that may involve considerable changes in the trophic level at which an organism feeds.

The effect of changing organism size on food chain production can be demonstrated by considering a three-species food chain analogous to the one described above except that the intermediate species now represents a more realistic organism, one which undergoes somatic growth and produces offspring at a size smaller than itself (Fig. 1B). Production consists of both somatic growth and reproduction. Their effect on food chain transfer can be demonstrated by deriving expressions for size-corrected production at the top of the food chain (P_3^*) and size-corrected consumption at the bottom ($C_2^* = W_1^{\epsilon}C_2$). Considering only somatic growth first, C_2^* can be calculated from a more precise definition of particle-size-conversion efficiency:

$$(5) \quad \epsilon = \frac{\log (dC_j/dP_j)}{\log (W_j/W_i)}$$

which gives

$$(6) \quad W_j^{\epsilon} \frac{dP_j}{dt} = W_i^{\epsilon} \frac{dC_j}{dt}.$$

Using equation 6, and because W_1 remains constant, the rate of change of C_2^* during somatic growth is given by

$$(7) \quad \frac{dC_2^*}{dt} = \frac{d(W_1^{\epsilon}C_2)}{dt} = W_1^{\epsilon} \frac{dC_2}{dt} = W_2^{\epsilon} \frac{dP_2}{dt}.$$

Similarly, the rate of change of P_3^* is given by

$$(8) \quad \frac{dP_3^*}{dt} = \frac{d(W_3^{\epsilon}P_3)}{dt} = W_3^{\epsilon} \frac{dP_3}{dt} = W_2^{\epsilon} \frac{dC_3}{dt}.$$

During somatic growth, the rate of production (dP/dt, as in equation 7) is given by NdW/dt (where N = number of animals) and the rate of elimination of biomass is given by $-WdN/dt$ (see, e.g., Gillespie and Benke 1979). In our case, the rate of elimination of species 2 ($-W_2dN_2/dt$) is equivalent to the rate of consumption by species 3 (dC_3/dt). Consequently, consumption of species 1 and production of species 3 are given by

$$(9) \quad (C_2^*)_{\text{growth}} = \int W_2^{\epsilon} N_2 \frac{dW_2}{dt}\, dt$$

$$(10) \quad (P_3^*)_{\text{growth}} = \int -W_2^{1+\epsilon} \frac{dN_2}{dt}\, dt.$$

I will now derive expressions for C_2^* and P_3^* for reproduction, so that the combined effects of somatic growth and reproduction can be demonstrated. During reproduction, if all production consists of egg production rather than growth, W_2 is constant. Furthermore, if we assume that the biomass of eggs produced is equivalent to the biomass of eggs produced by the previous generation (B_{2o}), then consumption of species 1 during reproduction by species 2, on a size-corrected basis, is

$$(11) \quad (C_2^*)_{\text{reproduction}} = W_1^{\epsilon}C_2 = W_{2r}^{\epsilon}P_2 = W_{2r}^{\epsilon}B_{2o}$$

where W_{2r} is the size of reproducing individuals of species 2. After reproduction and growth are complete, the final biomass (B_{2f}) of species 2 leads to production of species 3 equivalent to

$$(12) \quad (P_3^*)_{\text{final}} = W_3^{\epsilon}P_3 = W_{2f}^{\epsilon}C_3 = W_{2f}^{\epsilon}B_{2f}$$

where W_{2f} is the final size of species 2. Combining equations 9 and 11 and 10 and 12 gives total consumption of species 1 and production of species 3, respectively, as a function of the growth and mortality curves for species 2, all on a size-corrected basis:

$$(13) \quad C_2^* = W_{2r}^{\epsilon}B_{2o} + \int W_2^{\epsilon} N_2 \frac{dW_2}{dt}\, dt$$

$$(14) \quad P_3^* = W_{2f}^{\epsilon}B_{2f} + \int -W_2^{1+\epsilon} \frac{dN_2}{dt}\, dt.$$

Combining equations 13 and 14 gives

$$(15) \quad C_2^* = P_3^* + W_{2r}^{\epsilon}B_{2o} - W_{2f}^{\epsilon}B_{2f} + \int W_2^{\epsilon} \frac{dB_2}{dt}\, dt.$$

The last term in equation 15 is obtained because $dB/dt = d(NW)/dt = NdW/dt + WdN/dt$.

Equation 15 indicates that if $W_{2r} \approx W_{2f}$ and if dB_2/dt is equal to 0 (and consequently $B_{2o} = B_{2f}$), then $C_2^* \approx P_3^*$. Therefore, if mortality is sufficient during growth to compensate for increased organism size and to result in no net change in cohort biomass during growth, equation 15 simplifies to the same relationship obtained for the three-step food chain where species 2 is of constant size (i.e. equation 4) (Fig. 1A). It is possible, therefore, to substitute the assumption of constant size with the less restrictive assumption of constant cohort biomass for intermediate members of a food chain.

Equations 13, 14, and 15 can be compared with conventional equations for calculating production. Production (P) is production of eggs plus production due to somatic growth giving

$$(16)\quad P_2 = B_{2o} + \int N_2 \frac{dW_2}{dt}\, dt.$$

Equation 16 is analogous to equation 13, but omitting W^{ϵ}. Whereas equation 16 gives production, equation 13 is an estimate of the food consumption required to support this production. Biomass production can also be calculated from biomass eliminated. The total biomass eliminated for species 2 ($E_2 = C_3$) is elimination during growth plus elimination of the final size-class giving

$$(17)\quad E_2 = B_{2f} + \int -W_2 \frac{dN_2}{dt}\, dt.$$

Equation 17 is analogous to equation 14, but whereas equation 17 gives elimination for species 2, equation 14 gives production at higher trophic levels, which can be supported as a result of elimination of species 2. Combining equations 16 and 17 gives an equation analogous to equation 15, except that the integral does not contain W^{ϵ}_2, thereby permitting integration and yielding ΔB_2, which is equal to $B_{2o} - B_{2f}$. Consequently, $P_2 = E_2$, but C^*_2 is not necessarily equal to P^*_3. Note that the similarity in equations 13–17 permits calculation of P^* and C^* from the same data that one normally used to calculate production (P or E), provided an estimate of ϵ is available.

Longer Food Chains and Food Webs

I will now show how equations 13, 14, and 15 relate to more realistic food chains, and food webs, where complex species interactions exist and where few species contain individuals of constant size. A food chain containing four species, two of which vary in size and in which one of variable size feeds on another of variable size, is shown in Fig. 1C. Again, an organism of constant size is situated both on top and on the bottom of the food chain. Using arguments analogous to those used in the derivation of equation 15, it can be shown that the difference between size-corrected consumption at the bottom of the food chain (C^*_2) and size-corrected production at the top (P^*_5) is given by

$$(18)\quad C^*_2 = P^*_5 + W^{\epsilon}_{2r}B_{2o} - W^{\epsilon}_{2f}B_{2f} + W^{\epsilon}_{4r}B_{4o} - W^{\epsilon}_{4f}B_{4f} + \int W^{\epsilon}_2 \frac{dB_2}{dt}\, dt + \int W^{\epsilon}_4 \frac{dB_4}{dt}\, dt.$$

Derivation of equation 18 is more complex than derivation of equation 15 and is therefore not shown here (see Appendix A). However, determination of C^*_2 and P^*_5 for a five-species food chain, where species 1, 3, and 5 are of constant size and species 2 and 4 vary in size (Fig. 1D), is relatively simple. For this model we can calculate consumption of species 1 and production of species 3 from equations 13 and 14.

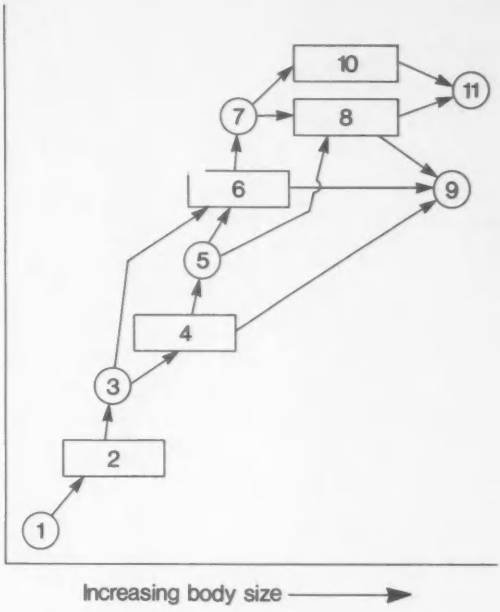

FIG. 2. An example of a possible "real world" food chain. Rectangles represent "real" species in which individual size varies. Circles represent hypothetical species in which all individuals are of constant size. Circles are inserted between real species to simplify the mathematics of calculating production (see text).

Similarly, we can calculate consumption of species 3 and production of species 5 from equations 13 and 14 after changing subscripts 2 and 3 to 4 and 5, respectively. Setting production of species 3 equal to consumption of species 4 (i.e. $P^*_3 = W^{\epsilon}_3 P_3 = W^{\epsilon}_3 C_4 = C^*_4$) and combining these equations gives equation 18. In other words, the relationship between production at the top of the food chain and consumption at the bottom is identical for the four- and five-species models shown in Fig. 1. However, production and consumption in the five-species model are easier to calculate than in the four-species model, because this can be done by using equation 15 twice. It is possible, therefore, to calculate the relationship between the production at the top and consumption at the bottom of a food chain containing many species of variable sizes by inserting "hypothetical" species of constant size in between each pair of species with variable sizes and calculating production as if it passed through these hypothetical species.

The above concepts can be expanded to model real life situations. For example, Fig. 2 shows a possible model for an ecosystem of five species, all of which undergo both somatic growth and reproduction. The circles represent hypothetical species, of constant body size, inserted to simplify calculation procedures. If production is calculated over a full year, and it is assumed that the biomass and sizes of organisms return to approximately equal values at 1-yr intervals, then

consumption of species 1 and production of species 9 and 11 are related by

$$(19)\quad C_2^* = P_9^* + P_{11}^* + \Sigma W_{ir}^{\epsilon} B_{io} - \Sigma W_{if}^{\epsilon} B_{if} + \Sigma \int W_i^{\epsilon} \frac{dB_i}{dt}\, dt = P_9^* + P_{11}^* + \Sigma C_i^* - \Sigma P_i^*$$

where W_{ir} and W_{if} represent the size at reproduction and final size, respectively, for each species, B_{io} and B_{if} represent initial and final cohort biomasses, and C_i^* and P_i^* represent size-corrected consumption and size-corrected production for each species (i refers to all real species, indicated by rectangles in Fig. 2). The integral accounts for changes in cohort biomass during somatic growth.

The contribution each species makes individually and the food each species utilizes within this ecosystem are given by equations 13 and 14 (with appropriate subscript changes). Equation 19 represents the overall relationship, which is simply the sum of contributions and food requirements for each species. The model in Fig. 2 contains production for two "species" at the top of the food chain. One of these (e.g. "species" 9) can represent production lost due to natural mortality (e.g. adult fish washing up on shore after spawning) and the other can represent commercial available production. In a real life situation the total production lost due to natural mortality may be difficult to estimate. Use of equation 19 therefore provides an estimate of "potential" fish production at the top of the food chain ($P_9^* + P_{11}^*$) rather than actual fish production (P_{11}^*). In practice, some of the production resulting in natural mortality may be recovered through recycling by a decomposer community, so that actual fish production may be greater than P_{11}^* but still less than potential fish production. Note that equation 19 does not require identification of which species feed on which other species. Consequently, application of equation 19 can provide estimates of production at the top of a food web from data on production at the bottom of the food web, and the only information required is that normally utilized in calculating production for individual species and some knowledge of the particle-size-conversion efficiency for the ecosystem.

Mysis Production

Lake Ontario

Biomass production of *Mysis relicta* in the Great Lakes provides a useful example for demonstrating the concepts of size-corrected production and consumption (equations 13 and 14). However, to show the parallelism between the calculation of production in the conventional manner (equations 16 and 17) and calculation of size-corrected production and consumption, I will first calculate mysid production in the conventional manner.

For calculating production, I used the size-frequency data of Carpenter et al. (1974) for Lake Ontario. Dr N. H. F. Watson (Bedford Institute of Oceanography, Dartmouth, N.S.) kindly provided me with the original size-frequency information. *Mysis relicta* does not produce discrete cohorts in Lake Ontario, so I calculated production from a variation

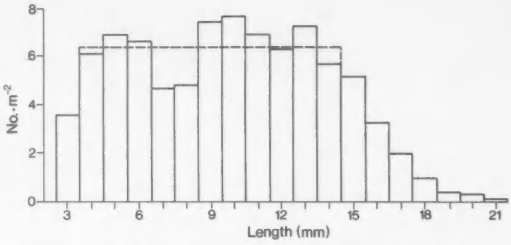

FIG. 3. Mean number of *M. relicta* within each size-class over 1 m^2 in Lake Ontario. Broken line represents the mean of the 4- to 14-mm size-classes (= 6.416 mysids·m^{-2}). (Data from Carpenter et al. 1974)

of the size-frequency method used by Sell (1982) for this same species in Lakes Michigan and Huron. I first calculated the average, over three cruises, of the number of animals present in each size-class (Fig. 3). I then used Sell's (1982) growth rate curve to calculate time spent in each stage. This curve (length (mm) = age (mo) + 3) fits nicely through the length–age relationship for *M. relicta* in Lake Michigan (Morgan and Beeton 1978). A full growth rate curve cannot be developed from the data of Carpenter et al. (1974) for Lake Ontario, although they did obtain a peak in abundance at around 4 to 5 mm in April and another peak centering around 11 mm in November, suggesting a growth rate similar to the Lake Michigan animals. A growth rate of 1 mm/mo means that the total number of animals passing through a 1-mm size-class in 1 yr (N in equations 16 and 17) is 12 times the mean number in that size-class throughout the year. Therefore, N is estimated at 12 times the numbers indicated in Fig. 3. Note that N is essentially constant for all size-classes from 4 to 14 mm in length. This suggests that almost no mortality occurs until the animals are over 14 mm long. If the growth rate estimate is correct, then the cases of increasing N with increasing size in Fig. 3 (which in theory is impossible, since mortality cannot be negative) are probably due to sampling or measuring errors, possibly as a result of the fact that animals were collected on only three cruises. I have therefore averaged frequency for size-classes 4–14 (mean = 6.416·m^{-2}, indicated in Fig. 3), which gives an N of 76.99·m^{-2}·yr^{-1} over this size range. Mysids 3 mm long were also assumed to have N = 76.99. The lower frequency in Fig. 3 would result if their size range did not cover a full millimetre (i.e. newly hatched individuals are approximately 3 mm, not 2.5 mm). Mysids larger than 14 mm were assumed to have N exactly equal to 12 times the abundance in Fig. 3. To estimate mysid weight in each size category, I used Sell's (1982) regression (log dry weight (mg) = 3.02 log length (mm) + log 0.00176).

To calculate production from equation 16 or 17, the integral can be broken down to equal the sum of all the integrals between one size-class and the next. For simplicity, I chose to assume that both growth and mortality are logarithmic ($dW/dt = gW$; $dN/dt = -mN$) from one size-class to the next, giving

$$(20)\quad P_{(a\text{ to }b)} = \frac{g(B_b - B_a)}{(g - m)} = \frac{(B_b - B_a)\ln(W_b/W_a)}{\ln(B_b/B_a)}$$

TABLE 1. Mean number of *M. relicta* within each cohort and the modal length of that cohort in Lake Superior. Numbers in parentheses indicate the numbers estimated from the individual cruises and used to obtain the average. Also shown is the size range summed to obtain estimates of cohort numbers.

Time	N (number·m^{-2})	Modal length (mm)	Size range (mm)
May–July (1st yr)	105.7(107.1, 96.3, 113.6)	3(3 in June, 4 in July)	3–5(May) 3–6(July)
October (1st yr)	105.7(107.1, 96.3, 113.6)	6.5	4–10
May–July (2nd yr)	54.6(51.9, 57.2)	10	6–14(May) 7–15(July)
October (2nd yr)	30.9	12.5	10–17
May–July (3rd yr)	2.2(3.2, 1.2)	16	≥15(May) ≥16(July)
October (3rd yr)	0.7	18	≥18

and similarly

$$(21)\quad E_{(a\text{ to }b)} = \frac{m(B_b - B_a)}{(g - m)} = \frac{(B_b - B_a)\ln(N_a/N_b)}{\ln(B_b/B_a)}$$

where B_a and B_b are the biomasses of size-groups a and b, respectively. Equation 20 is equivalent to equations given by several other authors (e.g. LeBlond and Parsons 1977; Gillespie and Benke 1979).

I calculated production from both equations 16 and 17. Using equation 16, I summed all estimates of production from one size-class to the next (equation 20) and added the biomass of offspring produced (B_{2o}). B_{2o} was estimated from the weight of a 3-mm mysid multiplied by the number of mysids produced per year (76.99·m^{-2}·yr^{-1}). Similarly, I calculated production from elimination using equation 17 by summing all estimates of elimination from one size-class to another (equation 21) and adding the final biomass (number of animals passing through the 21-mm size-group times the weight of a 21-mm animal). Elimination was 0 up to the 14-mm size-group because no measurable mortality occurred up to this point. Total yearly production and elimination were identical, as expected, and equal to 0.642 g·m^{-2}·yr^{-1}. This gave a production to biomass ratio of 2.83, similar to the P/B ratio calculated by Sell (1982) for *M. relicta* in Lake Huron, also using the data of Carpenter et al. (1974). Although my P/B ratio is similar, I estimated a lower production value than did Sell (1.5 g·m^{-2}·yr^{-1}), in spite of the larger number of mysids found in Lake Ontario as compared with Lake Huron (Carpenter et al. 1974). This is because I calculated production averaged over the entire lake, whereas Sell (1982) calculated production for stations over 90 m in depth only. The mean number of mysids in Lake Ontario was 86·m^{-2} whereas abundance at the deepest station was 419·m^{-2} (Carpenter et al. 1974), indicating that production at the deepest station may be as much as five times the lakewide average (assuming similar P/B ratios).

LAKE SUPERIOR

Mysis production in Lake Superior provides a valuable comparison with the Lake Ontario data because in Lake Superior discrete cohorts can be identified, making it unnecessary to rely on an estimated growth curve. I again used the data of Carpenter et al. (1974), supplied by Dr Watson. Mysids in Lake Superior were collected on three cruises, one at the end of May, one in early July, and one in October. The May and July cruises provide almost identical size-frequency distributions (see Fig. 3 of Carpenter et al. 1974), indicating little growth during this short period. Consequently, production within this time interval was not calculated separately. Two cohorts are clearly visible at any time, which permitted me to calculate the total number of animals within a cohort. I estimated the size range of the largest animals (a third cohort) from the growth rate of the smaller animals. The length and abundance of the organisms in the greater than 15-mm size-classes (Table 1) are somewhat subjective, but errors in their estimation should have little effect on production calculations because of their minor contribution to the total mysid population. The abundance of mysids in the smallest cohort was estimated at 107.1·m^{-2} in late May, 96.3·m^{-2} in early July, and 113.6·m^{-2} in October, suggesting that no measurable mortality occurred during this time interval. Consequently, I averaged these three numbers to obtain a mean estimate of numbers from June to October. The numbers of animals in the two larger cohorts in June were obtained from the average of the May and July cruises. The lack of mortality from June to October for the smallest cohort is similar to the situation in Lake Ontario, supporting my previous assumption of no mortality for the younger animals. Significant mortality in Lake Superior appears to occur primarily during the winter months (Table 1).

From the data in Table 1, I calculated production using equations 16 and 17. I summed production from June to October and October to June. Production and elimination for each cohort within one time interval were calculated using equations 20 and 21, respectively. B_a and B_b now refer to cohort biomasses at subsequent times rather than biomasses at adjacent size-classes. Initial and final biomasses (as required in equations 16 and 17) were calculated from N and W for the 3- and 18-mm animals in Table 1, again using Sell's (1982) length–weight relationship. Production and elimination were

equal to 0.263 $g \cdot m^{-2} \cdot yr^{-1}$. The production to biomass ratio for Lake Superior was 1.54.

Size-Corrected Consumption and Production of *Mysis*

The data used to calculate *Mysis* production in Lakes Ontario and Superior can also be used to calculate size-corrected production and consumption. However, an estimate of particle-size-conversion efficiency (ϵ, equations 1 and 5) is required. We have recently calculated the average ϵ for the Lake Ontario pelagic ecosystem using contaminants data (Borgmann and Whittle 1983) and will use this value for the calculations here ($\epsilon = 0.26$).

In a manner analogous to that used for calculating production in the conventional fashion, equations 13 and 14 can be applied by breaking the integral down to equal the sum of all the integrals between one size-class and the next. If we again assume that both growth and mortality are logarithmic from one size-class to the next ($dW/dt = gW$; $dN/dt = -mN$), then consumption from one size-class (a) to the next (b) is given by the integral in equation 13 and is equal to

$$(22)\quad (C_2^*)_{(a \text{ to } b)} = \int W_2^{\epsilon} N_2 \frac{dW_2}{dt}\, dt = \int W_2^{\epsilon} N_2 g W_2 dt = \int g B_2^* dt = \int g B_a^* e^{((1+\epsilon)g-m)t}\, dt = \frac{g(B_b^* - B_a^*)}{(1+\epsilon)g - m} = \frac{(B_b^* - B_a^*) \ln (W_b/W_a)}{\ln (B_b^*/B_a^*)}$$

where B_b is equal to the biomass in size-class b multiplied by the size raised to ϵ (i.e. $B_b^* = B_b W_b^{\epsilon}$). Similarly, $B_a^* = B_a W_a^{\epsilon}$. Potential production at higher trophic levels resulting from elimination of mysids from one size-class to the next is given by integration of $-W_2^{1+\epsilon} dN_2/dt$ (equation 14) and is equal to

$$(23)\quad (P_3^*)_{(a \text{ to } b)} = \frac{m(B_b^* - B_a^*)}{(1+\epsilon)g - m} = \frac{(B_b^* - B_a^*) \ln (N_a/N_b)}{\ln (B_b^*/B_a^*)}.$$

Equations 22 and 23 are analogous to equations 20 and 21, respectively, but give consumption and production estimates on a size-corrected basis. Summing size-corrected production and consumption over all size-classes gives the values summarized in Table 2. W_{2r}, the size of breeding adults, was assumed to represent animals 15 mm in length or larger. A minimum estimate of $W_{2r}^{\epsilon} B_{2o}$ is obtained by assuming that all reproduction occurs at 15 mm, and a maximum value is obtained by assuming that all reproduction occurs within the largest size-class. I used an intermediate value between these two extremes to estimate $W_{2r}^{\epsilon} B_{2o}$. As seen in Table 2, uncertainty in W_{2r} does not significantly affect estimates of C_2^*. Estimates of P_3^* are greater than C_2^* by 24–25% (Table 2).

The size-corrected consumption and production provide estimates of food consumed by mysids and potential fish production for fish feeding on mysids. If, for example, mysids consumed zooplankton at approximately 10^{-6} g each, total consumption would be about $C_2 = C_2^*/W_1^{\epsilon} = C_2^*/(10^{-6})^{0.26} = 5.45$ $g \cdot m^{-2} \cdot yr^{-1}$ in Lake Ontario and 1.76 $g \cdot m^{-2} \cdot yr^{-1}$ in Lake Superior. Potential fish production that could result from mysid elimination can be calculated for, e.g. 10 g (dry wt) fish, and would equal $P_3^*/10^{0.26} = 0.103$ $g \cdot m^{-2} \cdot yr^{-1}$ in Lake Ontario and 0.0331 $g \cdot m^{-2} \cdot yr^{-1}$ in Lake Superior.

If mysid mortality were higher for younger animals and sufficient to prevent any significant change in cohort biomass as a cohort grew to maturity, then C_2^* would have been equal to P_3^*, and potential fish production in Lakes Ontario and Superior resulting from the same consumption of zooplankton would only have been 0.0824 and 0.0267 $g \cdot m^{-2} \cdot yr^{-1}$, respectively (i.e. $C_2^*/10^{0.26}$). In other words, the cohort growth and mortality curves result in a 24–25% net gain in production at higher trophic levels, above what would have occurred if mysid cohort biomass remained constant or if mysid size did not change appreciably from newborn to adult.

TABLE 2. Summary of size-corrected consumption and production for *M. relicta* in Lakes Ontario and Superior calculated from equations 13 and 14. All units are $g^{1.26} \cdot m^{-2} \cdot yr^{-1}$.

	Lake Ontario	Lake Superior
Size-corrected consumption		
$W_{2r}^{\epsilon} B_{2o}$	0.001 (0.0010–0.0013)[b]	0.0015 (0.0014–0.0016)[c]
$\int W_2^{\epsilon} N_2 \frac{dW_2}{dt}\, dt$[a]	0.149	0.0471
C_2^*	0.150	0.0486
Size-corrected production at higher trophic levels		
$W_{2f}^{\epsilon} B_{2f}$	0.007	0.0024
$\int -W^{1+\epsilon}{}_2 \frac{dN_2}{dt}\, dt$[d]	0.181	0.0578
P_3^*	0.188	0.0602
P_3^*/C_2^*	1.25	1.24

[a]Calculated from the sum of consumption over individual size classes in Fig. 3 and Table 1 using equation 22.

[b]Estimated range using W_r calculated for 15- to 21-mm-long animals.

[c]Estimated range using W_r calculated for 15- to 18-mm-long animals.

[d]Calculated from the sum of production over size-classes in Fig. 3 and Table 1 using equation 23.

Discussion

The model I have presented here (equations 15 and 19) incorporates the concepts of somatic growth and reproduction within an earlier model of biomass transfer up pelagic food webs. The initial model (Borgmann 1982) permitted estimation of production at any trophic level from data on production at any other trophic level if the average particle-size-

conversion efficiency was known. That model was derived by assuming that each species had a fixed size. My extension of the original model (i.e. equations 15 and 19) has two major benefits. First, it is no longer necessary to assume that organisms remain at a constant size during their life cycle. Production at the top of the food web can still be estimated from production at the bottom without any knowledge of production at any intermediate trophic level (equation 4). The underlying assumption is now that the cohort biomasses for all species at intermediate trophic levels do not change appreciably during their life cycles (i.e. $dB_2/dt = 0$, equation 15). If this assumption holds, then somatic growth and reproduction have no net effect on the efficiency of biomass transfer up the food web. Although this assumption may not be entirely true, it is more realistic than assuming organisms remain at one size.

The second benefit is that if data on changes in biomass are available for any species at an intermediate trophic level, then these data can be incorporated to provide an estimate of what effect (if any) somatic growth and reproduction by that species have on the efficiency of biomass transfer up the food web. My model is, in a sense, a holistic one, describing biomass flow through the whole ecosystem. However, it allows for the inclusion of data on single species, such as the cohort data often obtained when calculations of single-species production are made. I have used production by *M. relicta* to demonstrate this. The data in Fig. 3 and Table 1 provide a good example of the potential effect of somatic growth on food web efficiency because mortality appears to be negligible for the younger animals, and potential production at higher trophic levels results from elimination of mature or nearly mature mysids. Consequently, most of the mysid production appears to occur during somatic growth and each adult need produce relatively few offspring to perpetuate the population. The role of growth greatly outweighs the effect of reproduction, and overall size-corrected production exceeds consumption by 24–25% (Table 2). The estimates in Table 2 may have to be altered as more data on *M. relicta* become available, but they nevertheless provide a demonstration of how equations 13 and 14 can be applied. In natural waters most species would be expected to have greater mortality among the younger individuals, and consequently, somatic growth and reproduction would be expected to have a smaller impact on the efficiency of biomass transfer up pelagic food webs than predicted for *Mysis* from the data in Fig. 3 and Table 2.

My model allows for a considerable simplification in the analysis of pelagic food webs. The reason for this is the form of equation 19. If size-corrected consumption and production can be calculated for all of the intermediate trophic levels in a food web, as was done for the *Mysis* example here, then their total effect on biomass flow up the food web can be calculated by simply summing over all species. The use of the assumption that particle-size-conversion efficiency is constant eliminates the need to identify who feeds on what. Therefore, the exact structure of the food web need not be known. For example, equation 19 contains no terms that specify the nature of the trophic links in Fig. 2. It is also not necessary to measure how much food is consumed at any trophic level (e.g. food consumed by *Mysis* was not measured directly in the data presented here). It is assumed that this can be predicted from production and particle-size-conversion efficiency. It is therefore not necessary to collect detailed data on food consumption for intermediate trophic level organisms. It is only necessary to either collect data on changes in cohort biomass or else assume that cohort biomass remains constant.

All of the above calculations are based on the assumption that particle-size-conversion efficiency, ϵ, is relatively constant. This is obviously an approximation, as some deviation about a mean is to be expected (e.g. see Borgmann 1982). If a complete knowledge of conventional conversion efficiency (P/C), production, consumption, somatic growth, who feeds on what, etc., is available for all species in an ecosystem, then biomass flow in the ecosystem can be calculated using a conventional compartmentalized computer model. However, such complete information is never available, and all estimates of production and biomass flow up food chains, using any model, require assumptions about, and estimates of, parameters that often cannot be measured for all species. Under such conditions, choosing the right kinds of assumptions can greatly simplify the mathematics involved and reduce the total number of assumptions that need to be made when modeling biomass flow through an ecosystem. The assumption of a constant particle-size-conversion efficiency does this. It reduces the mathematics to the point where production for different-sized organisms and at different trophic levels is additive (i.e. equation 19) and permits estimation of the effects of reproduction and somatic growth in pelagic food chains. Furthermore, ϵ can be estimated from contaminant levels in these organisms (Borgmann and Whittle 1983). These advantages make the concept of particle-size-conversion efficiency a valuable tool in modeling pelagic ecosystems, even though the assumption of a constant ϵ in any ecosystem is only an approximation.

Acknowledgments

I thank Dr N. H. F. Watson for providing the data on *Mysis relicta*, Drs A. H. El-Shaarawi and C. K. Minns for reviewing the manuscript, and Anne Borgmann for her encouragement and many helpful comments on the manuscript.

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Appendix A

The major assumption used in the derivation of equation 19 is that insertion of a hypothetical species, which contains organisms of constant size only, between two species with variable body sizes (i.e. "real" organisms) does not affect the overall production equations. To prove this, I derive equation 18 from the four-species model in Fig. 1C below. Derivation of this equation from the five-species model is discussed in the text.

Equation 6 indicates that the rate of production of species 4, multiplied by W_4^ϵ, equals the rate of consumption of species 2 by species 4, multiplied by W_2^ϵ (species 3 does not exist in the four-species model) (Fig. 1C). If we combine production during somatic growth with reproduction, this gives

$$(24)\quad W_4^\epsilon \frac{dP_4}{dt} + W_{4r}^\epsilon \frac{dP_{4r}}{dt} = W_2^\epsilon \frac{dC_4}{dt} + W_{2f}^\epsilon \frac{dC_{4f}}{dt}$$

The first term in equation 24 represents production during somatic growth. Therefore, $dP_4/dt = N_4 dW_4/dt$. The second term represents production by reproducing adults at size W_{4r}. The total production during reproduction (i.e. the integral of dP_{4r}/dt) is the biomass of eggs produced (B_{4o}). The first term on the right of equation 24 represents consumption of all sizes of species 2 by species 4 except the largest individuals. The rate of biomass consumption (i.e. elimination) of species 2 is equivalent to $dC_4/dt = -W_2 dN_2/dt$. The last term on the right of equation 24 represents consumption of the largest individuals of species 2 (at size W_{2f}). Since this group must eventually be eliminated completely, it cannot be included with the previous term (i.e. the mortality rate, dN/Ndt, is infinite). However, the total elimination of these animals is their final biomass (B_{2f}). Therefore, substituting and integrating equation 24 gives

$$(25)\quad \int W_4^\epsilon N_4 \frac{dW_4}{dt} + W_{4r}^\epsilon B_{4o} = \int -W_2^\epsilon W_2 \frac{dN_2}{dt} + W_{2f}^\epsilon B_{2f}.$$

Equation 25 describes the relationship between production of species 4 and consumption of species 2. The relationship between consumption of species 1 by species 2 and production of species 2 is given by equation 13. The relationship between consumption of species 4 and production of species 5 is given by an equation analogous to equation 14, but with appropriate subscript changes:

$$(26)\quad P_5^* = W_{4f}^\epsilon B_{4f} + \int -W_4^{1+\epsilon} \frac{dN_4}{dt}\, dt.$$

Combining equations 25, 13, and 26 gives

$$\begin{aligned}(27)\quad C_2^* &= P_5^* + W_{2r}^\epsilon B_{2o} - W_{2f}^\epsilon B_{2f} + W_{4r}^\epsilon B_{4o} - W_{4f}^\epsilon B_{4f} \\ &\quad + \int W_2^\epsilon N_2 \frac{dW_2}{dt}\, dt + \int W_2^\epsilon W_2 \frac{dN_2}{dt}\, dt \\ &\quad + \int W_4^\epsilon N_4 \frac{dW_4}{dt}\, dt + \int W_4^\epsilon W_4 \frac{dN_4}{dt}\, dt \\ &= P_5^* + W_{2r}^\epsilon B_{2o} - W_{2f}^\epsilon B_{2f} + W_{4r}^\epsilon B_{4o} - W_{4f}^\epsilon B_{4f} \\ &\quad + \int W_2^\epsilon \frac{dB_2}{dt}\, dt + \int W_4^\epsilon \frac{dB_4}{dt}\, dt.\end{aligned}$$

Equation 27 is the same as equation 18, proving that insertion of hypothetical species between "real" species does not alter the final production equations, although it simplifies derivation of these equations.

Sexual Dimorphism in the Adipose Fin of Pacific Salmon (*Oncorhynchus*)

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BEACHAM, T. D., AND C. B. MURRAY. 1983. Sexual dimorphism in the adipose fin of Pacific salmon (*Oncorhynchus*). Can. J. Fish. Aquat. Sci. 40: 2019–2024.

Male adipose fins of *Oncorhynchus* species were 30–50% larger than those of same-sized females, the actual amount depending on the species. Accuracy of classification of the standards ranged from 87% in chinook salmon (*O. tshawytscha*) to 98% in pink salmon (*O. gorbuscha*). Testing the method on new samples usually resulted in an accuracy of at least 90% correct identification of sex for any species. Relative size of the adipose fin should allow for easy and accurate external identification of the sexes of silver-bright *Oncorhynchus*.

BEACHAM, T. D., AND C. B. MURRAY. 1983. Sexual dimorphism in the adipose fin of Pacific salmon (*Oncorhynchus*). Can. J. Fish. Aquat. Sci. 40: 2019–2024.

La nageoire adipeuse des mâles d'espèces du genre *Oncorhynchus* est de 30 à 50 % plus grosse que celle de femelles de même taille, le pourcentage dépendant de l'espèce. La précision dans la classification des normes est comprise entre 87 % pour le saumon chinook (*O. tshawytscha*) et 98 % pour le saumon rose (*O. gorbuscha*). En vérifiant la méthode sur de nouveaux échantillons, on obtient ordinairement une identification correcte du sexe, quelle que soit l'espèce, avec une précision d'au moins 90 %. La taille relative de la nageoire adipeuse serait un caractère externe permettant d'identifier facilement et correctement le sexe d'individus argentés du genre *Oncorhynchus*.

Received April 26, 1983
Accepted August 2, 1983

Reçu le 26 avril 1983
Accepté le 2 août 1983

PACIFIC salmon (*Oncorhynchus*) develop secondary sexual characteristics just before or at the time that they enter freshwater to spawn. At this time, males develop elongated upper jaws, a phenomenon well documented by Briggs (1953) and Vladykov (1962). They may also develop a hump-backed appearance, and both males and females may develop distinctive spawning colors. The marked degree of sexual dimorphism in head morphology, body shape, and color at spawning time allows for easy identification of males and females.

During ocean residence, before the development of secondary sexual characteristics, all *Oncorhynchus* species are silver bright in color, and there is no obvious sexual dimorphism. Morton (1965) stated that "It is very difficult or almost impossible to distinguish externally the sexes of any species of *Oncorhynchus* taken from the sea." Salmon in this silver-bright state are the most valuable, and there are extensive commercial fisheries that harvest salmon in this condition. It is frequently of interest to identify the sexes in these fisheries in order to improve management. It would also be of value to be able to determine externally the sex of an individual in tagging studies when fish are released alive. Internal examination of individuals to determine sex is not possible in tagging studies and in most salmon fisheries because of the processors' requirements for unmarked, high-grade salmon as a condition for sale of the fish. A method to externally determine the sex of individuals in this silver-bright state would be desirable.

Fin size in *Oncorhynchus* is not considered to be dependent on the state of sexual maturity of the individual. Vladykov (1963) noted anecdotally that the adipose fin in large spawning *Oncorhynchus* males is larger than in females. Weisel (1968) outlined the anatomy of the salmonid adipose fin but gave no indication that it was sexually dimorphic. McPhail and Murray (1979) used differences in adipose fin size to determine externally the sex of Dolly Varden (*Salvelinus malma*). In this paper we examine the possibility of using differences in adipose fin size to determine externally the sex of *Oncorhynchus* species. The five Northwest Pacific salmon species investigated were pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), and chinook salmon (*O. tshawytscha*).

Materials and Methods

We sampled the five species of *Oncorhynchus* in the autumn of 1982 at the locations outlined in Fig. 1. Measurements were taken from freshly killed individuals. For each individual, sex was recorded after internal inspection, postorbital–hypural length (distance from posterior edge of the orbit to the end of the hypural plate) to the nearest 0.5 cm was determined with a hypural stick, and adipose fin length to the nearest millimetre was determined with vernier calipers. The length of the adipose fin was measured as the

Printed in Canada (J7340)
Imprimé au Canada (J7340)

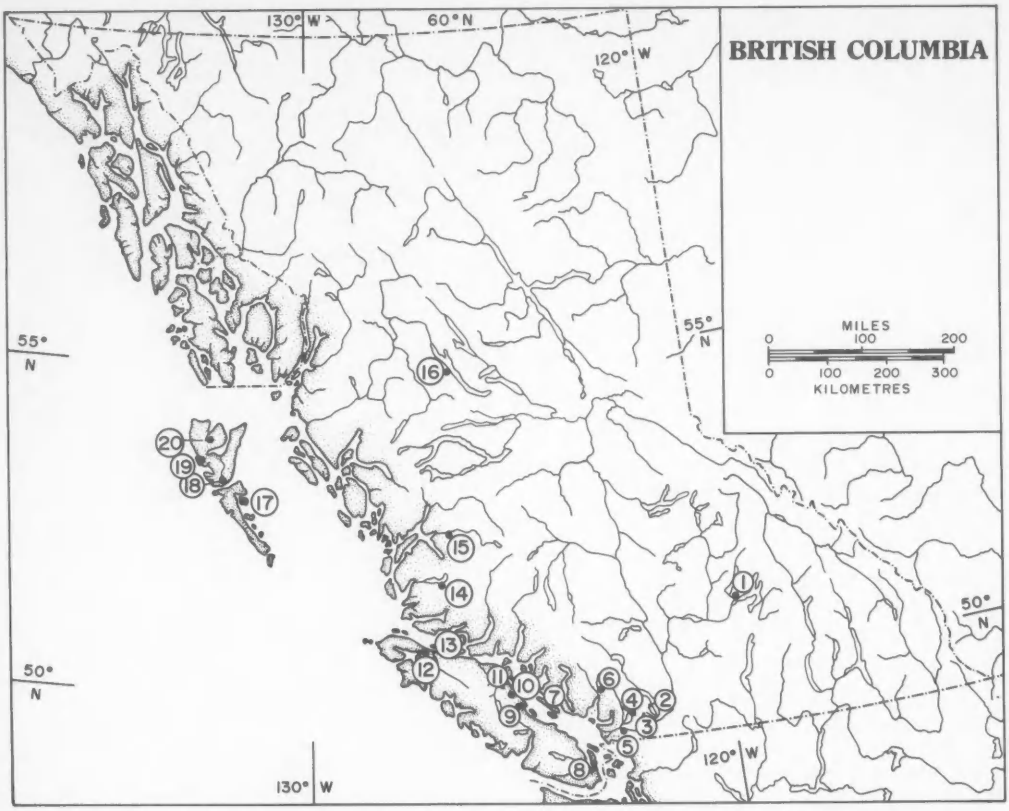

FIG. 1. Areas in British Columbia where measurements from *Oncorhynchus* species were collected. Locations listed in ascending order are (1) Adams R., (2) Weaver Cr., (3) Chehalis R., (4) Blaney Cr., (5) Fraser R., (6) Tenderfoot Cr., (7) Saltery Bay test fishery, (8) Cowichan test fishery, (9) Puntledge R., (10) Black Cr., (11) Quinsam R., (12) Cluxewe R., (13) Alert Bay test fishery, (14) Owikeno Lake, (15) Bella Coola R., (16) Fulton R., (17) Mathers Cr., (18) Delta Cr., (19) Mercer Cr., and (20) Naden Cr.

maximum distance from the origin of the base as indicated by the absence of scales to the most posterior portion of the lobe (Fig. 2).

In our analysis, adipose fin measurements of both males and females were standardized separately to the overall mean length of all individuals for each species. This minimized the variability as a result of allometric growth and differences in mean size of the individuals among areas (Gould 1966). We adjusted measurements by the method outlined by Ihssen et al. (1981):

$$(1) \quad M_t = M_0\left(\frac{\bar{L}}{L_0}\right)^b$$

where M_t = transformed adipose fin length, M_0 = observed adipose fin length, $\bar{L}$ = overall mean length for males and females combined for all areas, L_0 = observed length, and b = regression coefficient of log M_0 on log L. There were separate regressions for males and females (different regression coefficients) for each species. To investigate differences in adipose fin size between the sexes, we conducted two-way analyses of variance (BMDP2V) with sex and sampling location as the indices. To obtain classification functions for classification of new individuals, we used discriminant analysis (BMDP7M).

Results

The salmon sampled varied in size among and within sampling locations for each species. To compare differences in adipose fin size between males and females, it was first necessary to correct all adipose length measurements to those of a fish of standard length for each species. The allometric relationship between adipose fin length and postorbital–hypural length was determined for each sex for each species and also for both sexes combined (Table 1). By using equation 1 and the regression coefficients outlined in Table 1, we standardized adipose fin measurements for all individuals examined and for new individuals tested subsequently.

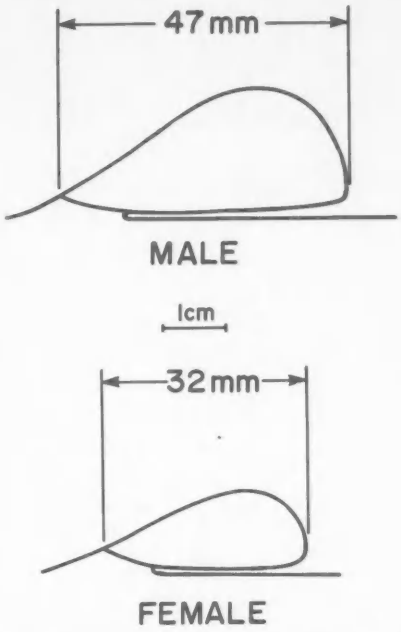

FIG. 2. Observed adipose fin shapes of male and female sockeye salmon 51.0 cm postorbital–hypural length. Note that the male adipose fin is longer and higher than the female adipose fin.

TABLE 1. Allometric regressions for $\ln AF = \ln a + b \ln L$, where AF is adipose fin length, L is postorbital–hypural length, $\ln a$ is a regression constant, b is the regression coefficient, SE is its standard error, and r is the correlation coefficient.

Species	Sex	N	$\ln a$	b	SE	r
Pink	Male	94	−3.01	1.10	0.12	0.70
	Female	83	−3.77	1.17	0.28	0.42
	Total	177	−4.98	1.40	0.25	0.39
Chum	Male	712	−4.04	1.23	0.06	0.59
	Female	667	−3.90	1.16	0.08	0.49
	Total	1379	−5.38	1.42	0.09	0.40
Sockeye	Male	207	−2.54	1.01	0.05	0.80
	Female	253	−2.11	0.89	0.08	0.58
	Total	460	−1.66	0.84	0.07	0.48
Chinook	Male	210	−3.60	1.18	0.06	0.79
	Female	180	−3.05	1.06	0.13	0.53
	Total	390	−0.13	0.63	0.07	0.43
Coho	Male	163	−4.70	1.36	0.06	0.86
	Female	180	−5.97	1.52	0.08	0.81
	Total	343	−4.27	1.26	0.08	0.63

TABLE 2. Mean adipose fin lengths (mm) of *Oncorhynchus* species examined. Adipose fin lengths were standardized to a body length of 386 mm for pink salmon, 592 mm for chum salmon, 461 mm for sockeye salmon, 661 mm for chinook salmon, and 522 mm for coho salmon.

Species	Sex	Location	N	Adipose	SD
Pink	Male	Cluxewe	44	36.0	3.1
		Quinsam	50	35.2	3.0
		Total	94	35.6	3.1
	Female	Cluxewe	33	23.5	3.1
		Quinsam	50	24.5	2.6
		Total	83	24.1	2.9
Chum	Male	Alert Bay	428	44.8	4.5
		Puntledge	159	43.8	4.9
		Blaney	46	48.4	4.6
		Cowichan	79	46.1	5.7
		Total	712	45.0	4.8
	Female	Alert Bay	711	33.0	3.4
		Puntledge	137	31.7	3.3
		Blaney	49	33.8	3.0
		Cowichan	70	32.2	4.1
		Total	667	32.7	3.5
Sockeye	Male	Fulton	24	35.9	5.2
		Owikeno	30	42.6	3.3
		Mathers	24	39.0	4.2
		Mercer	25	40.3	3.6
		Naden	23	42.7	3.6
		Delta	25	39.9	3.6
		Adams	56	37.9	2.7
		Total	207	39.5	4.2
	Female	Fulton	77	28.8	3.7
		Owikeno	29	32.1	4.1
		Mathers	26	30.2	3.3
		Mercer	25	25.3	3.9
		Naden	27	28.9	2.3
		Delta	25	29.5	2.5
		Adams	44	30.4	2.5
		Total	253	29.3	3.7
Chinook	Male	Chehalis	60	63.0	6.6
		Puntledge	150	57.6	6.9
		Total	210	59.1	7.2
	Female	Chehalis	60	49.7	5.7
		Puntledge	120	43.2	3.9
		Total	180	45.3	5.5
Coho	Male	Bella Coola	16	47.6	3.5
		Puntledge	71	44.1	4.0
		Tenderfoot	7	45.7	2.9
		Fraser	69	42.8	4.2
		Total	163	44.0	4.2
	Female	Bella Coola	14	33.7	2.7
		Puntledge	76	33.1	3.5
		Tenderfoot	7	35.4	2.6
		Fraser	83	33.7	3.9
		Total	180	33.5	3.6

SEXUAL DIMORPHISM

After the adipose fin lengths of both males and females had been corrected to that of a fish of standard length (386 mm for pink salmon, 592 mm for chum salmon, 461 mm for sockeye salmon, 661 mm for chinook salmon, and 552 mm for coho salmon), we used analysis of variance to examine variability in adipose fin length among sampling locations and between

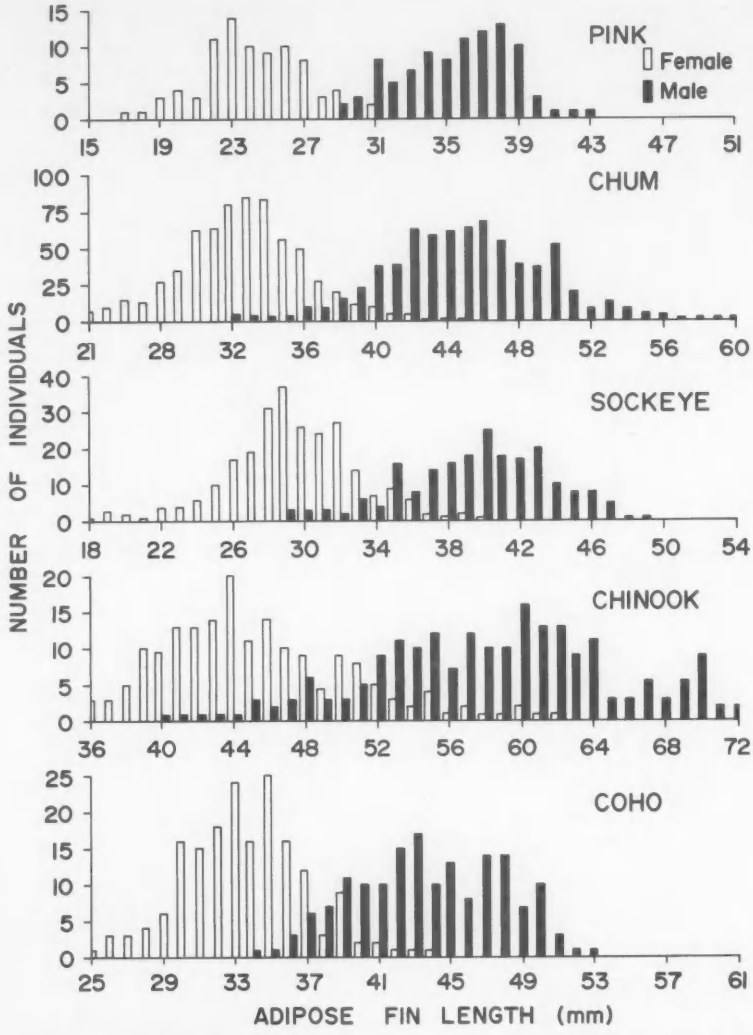

FIG. 3. Frequencies of adipose fin length for male and female pink, chum, sockeye, chinook, and coho salmon.

the sexes. At the standardized postorbital–hypural length, male pink salmon had significantly larger adipose fins (35.6 mm) than did females (24.1 mm) ($F = 652$; df = 1, 173; $P < 0.01$) (Table 2). Male adipose fins were, on average, 48% larger than those of females. Male pink salmon from Quinsam and Cluxewe rivers also had similar-sized adipose fins, as did females from the same rivers ($F = 0.04$, $P > 0.20$). Male chum salmon had larger adipose fins than did females ($F = 1829$; df = 1, 137; $P < 0.01$). Male adipose fins were, on average, 38% larger than those of females. Adipose fin size also varied among locations sampled ($F = 17$; $P < 0.01$), possibly indicative of small differences in adipose fin size among stocks.

The trend for males to have larger adipose fins than females was also evident for sockeye (Table 2). In the seven areas surveyed, the adipose fins of male sockeye were an average of 35% larger than those of females. As well as a significant difference in adipose fin size between the sexes ($F = 914$; df = 1, 446; $P < 0.01$), there were differences among stocks ($F = 14$; $P < 0.01$). Even so, males consistently had larger adipose fins than females in all stocks surveyed. The adipose fins on male chinook salmon were 30% larger overall than on

TABLE 3. Relative proportions of adipose fin length to body length in *Oncorhynchus*. Values listed are the species' mean divided by the standardized lengths in Table 2.

Sex	Species	% of standardized length
Male	Pink	9.2
	Chum	7.6
	Sockeye	8.6
	Chinook	8.9
	Coho	8.4
Female	Pink	6.2
	Chum	5.5
	Sockeye	6.4
	Chinook	6.9
	Coho	6.4

TABLE 4. Results of classification of individuals by discriminant analysis. Areas sampled are outlined in Table 2.

Species	Sex	*N*	% correct
Pink	Male	94	98
	Female	83	98
Chum	Male	695	93
	Female	684	95
Sockeye	Male	205	89
	Female	255	92
Chinook	Male	210	87
	Female	180	87
Coho	Male	163	90
	Female	180	91

similar-sized females ($F = 460$; df = 1, 386; $P < 0.01$) (Table 2). Chinook salmon of both sexes from the Chehalis River, a tributary of the Fraser River, had larger adipose fins than did chinook salmon from Puntledge River on Vancouver Island ($F = 85$; $P < 0.01$). Finally, the trends in coho salmon were the same, with males having larger adipose fins than same-size females ($F = 286$; df = 1, 335; $P < 0.01$), and with male adipose fins an average of 31% larger than those of females. Stock differences in adipose fin size of coho were again apparent ($F = 4.5$; $P < 0.01$).

Variability in adipose fin size was greater in males than in females for all five species (Table 2; Fig. 3). The smallest degree of overlap in adipose fin size in males and females occurred in pink salmon, whereas the greatest amount occurred in chinook salmon (Fig. 3). Chinook males may return to spawn after residing only one summer in the ocean, and these so called "jack" males are smaller than older returning males and all females. The adipose fins on these jack males were noticeably smaller compared with those on older, mature males. These jack males account for the greater degree of overlap in adipose fin size between males and females in chinook salmon as compared with pink salmon, where all individuals return to spawn at age 2.

Considering relative size of the adipose fin, male pink salmon had proportionately the largest adipose fin, whereas female chum salmon had the smallest (Table 3). The adipose fin for both sexes of chum salmon was proportionately the smallest for the five species. Overall, adipose fins of males averaged about 8.5% of body length, whereas those of females averaged about 6.3%.

TABLE 5. Classification functions used to determine sex of new individuals. *AF* is adipose fin length (mm). Adipose fin lengths have previously been standardized to body lengths listed in Table 2. Sex is determined by the function with the higher value.

Species	Sex	Function
Pink	Male	$y = 3.98AF - 71.5$
	Female	$y = 2.70AF - 33.4$
Chum	Male	$y = 2.50AF - 57.0$
	Female	$y = 1.82AF - 30.6$
Sockeye	Male	$y = 2.55AF - 51.2$
	Female	$y = 1.89AF - 28.3$
Chinook	Male	$y = 1.40AF - 42.1$
	Female	$y = 1.08AF - 25.2$
Coho	Male	$y = 2.87AF - 63.9$
	Female	$y = 2.19AF - 37.4$

TABLE 6. Results using classification functions listed in Table 5 to identify sex of new individuals.

Species	Location	Sex	*N*	% correct
Pink	Puntledge	Male	8	100
		Female	49	100
Chum	Saltery Bay	Male	41	93
		Female	29	100
Sockeye	Weaver	Male	50	82
		Female	49	100
Chinook	Puntledge	Male (all)	30	63
		Male (>55 cm)	17	74
		Male (>60 cm)	15	88
		Female (all)[a]	30	90
Coho	Black Creek	Male	9	100
		Female	10	80

[a]All female chinook in the test sample were greater than 60 cm in postorbital–hypural length.

Adipose fin length of the sexes tended to have separate distributions, but there was overlap in these distributions (Fig. 3). Discriminant analyses were used to identify the sex of each individual based solely on adipose fin length. These analyses showed that the accuracy of the classification of the standards ranged from 87% in chinook salmon to 98% in pink salmon (Table 4). Except for chinook salmon, at least 90% of the individuals were correctly identified as to their sex based solely on the length of the adipose fin. Therefore, adipose fin size could be used to determine externally the sex of *Oncorhynchus* species.

TESTING THE METHOD

Samples from all five species not used in the construction of the classification functions provided an independent test of the method. The procedure for testing new fish for each species was as follows. After adipose fin lengths were

standardized to the appropriate body length (Table 2), by using the total allometric regression (Table 1), they were entered into the appropriate classification functions for the species as listed in Table 5. For example, the adipose fin length of a chum salmon was standardized to a body length of 592 mm, and this standardized value was used in both the male and female classification functions. The sex was determined by the function with the higher value.

The sex of the pink salmon in the sample was determined with 100% accuracy, and the overall accuracy for each species was usually 90% (Table 6). In chinook salmon, accuracy of the classification of males increased as jack males were excluded from the samples. The analyses indicated that it is possible to sex *Oncorhynchus* species externally with a high degree of accuracy using the size of the adipose fin.

Discussion

Sexual dimorphism has been described in adults of many salmonid species, especially in *Salmo* (Vladykov 1963; Morton 1965; Breder and Rosen 1966), but most of the dimorphisms are temporary and occur during the spawning season (Briggs 1953; Stoklosowa 1966). A dimorphism not dependent on the state of sexual maturity of the individual would be useful for practical fisheries management, hatchery operations, and some commercial applications. Gruchy and Vladykov (1968) reported that anal fin shape was sexually dimorphic in brown trout (*S. trutta*). The dimorphism was visible externally, present on individuals collected at all times of the year, and evident in small individuals. This dimorphism would obviously be quite useful for externally determining the sex of individual brown trout.

Relative size of the adipose fin has been used to distinguish species of salmonids. Schultz (1936) reported that the ratio of head length divided by adipose fin length could be used to distinguish between Rocky Mountain whitefish (*Prosopium williamsoni*) and the Oregon whitefish (*P. oregonium*). The adipose fin of *P. oregonium* was reported to be larger than that of *P. williamsoni*. However, Holt (1960) indicated that the two species were conspecific. It is possible that Schultz may have described sexual dimorphism in the adipose fin rather than species differences in *Prosopium*.

Adipose fins in *Oncorhynchus* have been the object of some investigations. Weisel (1968) outlined a thorough anatomy of the fin. Dahlberg and Phinney (1967) used adipose fin pigmentation for distinguishing between juvenile chinook and coho salmon in Alaska. The adipose fins of coho salmon were completely pigmented, whereas those of chinook salmon showed a clear area, generally near the anterior part of the base. It is thus possible to use the adipose fin for species identification in some juvenile *Oncorhynchus*. McPhail and Murray (1979) used the differences in adipose fin shape to determine externally the sex of bright Dolly Varden char (*S. malma*), which are not strikingly sexually dimorphic. In male Dolly Varden, however, the height of the adipose fin is greater than the free portion of its base and in females the height is equal to the free portion of its base. Scott and Crossman (1973) have outlined the relative sizes of the adipose fin in their descriptions of *Oncorhynchus* species. It is, however, not stated whether they were referring to the adipose fin of males or females in their descriptions. Moreover, sockeye salmon are described by them as having rather small adipose fins, but in our study, sockeye adipose fins were at least proportionately as large as in the other species. Also, they described chum salmon as having a large, fleshy adipose fin, but we found their adipose fins to be proportionately smaller than in the other species. We conclude that relative size of the adipose fin is a useful tool for externally determining the sex of *Oncorhynchus* species. The dimorphism was so marked that with experience it was usually possible to visually inspect the adipose fin to identify the sex of the individual correctly.

Future work might consider sexual dimorphism in adipose fin size of other salmonid genera, particularly if this technique is used for species or subspecies identification. Investigations could also be conducted to see if the sex of juvenile *Oncorhynchus* can be determined externally from adipose fin size.

Acknowledgments

Peter Withler, Dave Hahn, Gerry Buxton, Mark Zado, and Glen Worth assisted with the sampling, as well as Harry Genoe of the Puntledge River hatchery. Dr H. Mundie provided constructive suggestions on the manuscript. Lauri Mackie drafted the figures. The Publications Unit of the Pacific Biological Station prepared the manuscript.

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NOTES

Downstream and Lateral Transport of Nymphs of Two Mayfly Species (Ephemeroptera)

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CIBOROWSKI, J. J. H. 1983. Downstream and lateral transport of nymphs of two mayfly species (Ephemeroptera). Can. J. Fish. Aquat. Sci. 40: 2025 – 2029.

By releasing live and dead nymphs of two mayfly species, *Baetis tricaudatus* Dodds and *Ephemerella inermis* Eaton, into the water column of a river and catching them downstream in a series of contiguous nets, I estimated settling and lateral dispersal rates. Live animals settled over shorter distances than dead individuals, and became more widely laterally dispersed for any given distance downstream and mean current velocity. Transport of suspended organisms in a river in which mean current velocity increases with increasing distance from shore may produce a skewed cross-river benthic distribution of animals. The degree of skewness will depend on the current velocity gradient and on suspended animals' settling behavior.

CIBOROWSKI, J. J. H. 1983. Downstream and lateral transport of nymphs of two mayfly species (Ephemeroptera). Can. J. Fish. Aquat. Sci. 40: 2025 – 2029.

Des nymphes vivantes et mortes de deux espèces d'éphémères, *Baetis tricaudatus* Dodds et *Ephemerella inermis* Eaton, ont été libérées dans l'eau d'une rivière et capturées en aval dans une série de filets contigus, dans le but d'estimer les taux de déposition et de dispersion latérale. Les animaux vivants se sont établis sur le fond après avoir parcouru des distances plus courtes que les sujets morts et, à une distance en aval et une vitesse de courant moyennes données, se sont dispersés latéralement sur une plus grande superficie. Le transport d'organismes en suspension dans un cours d'eau dans lequel la vitesse de courant moyenne augmente en fonction de l'éloignement de la rive peut introduire un biais dans la distribution benthique des animaux d'une rive à l'autre. L'ampleur de ce biais dépendra du gradient de vitesses de courant et du comportement de fixation au fond des animaux en suspension.

Received March 28, 1983
Accepted July 15, 1983

Reçu le 28 mars 1983
Accepté le 15 juillet 1983

MOST lotic invertebrates occasionally become dislodged from the substrate and transported downstream. The rate of return to the stream bottom depends on the size and shape of each animal (McLay 1970; McKone 1975) as well as current velocity (Elliott 1971). Behavioral actions (swimming motions and thigmotactic responses to contact with the substrate) result in rapid settling rates for certain species (Elliott 1971), especially those frequently appearing in the drift (Ciborowski and Corkum 1980).

Most studies of settling behavior have been concerned with the distance animals are carried downstream; but lateral transport may also be important in determining subsequent benthic microdistribution. Ulfstrand (1968) postulated that cross-river movements could produce rapid changes in microdistribution of benthic populations. Lehmkuhl and Anderson (1972) reported that animals prone to drift are carried from riffles to backwaters at the stream margin during floods. However, earlier experimental studies have failed to evaluate the degree of lateral dispersal exhibited by animals released into the water column.

My objective was to determine settling rates, downstream movement, and lateral transport of the mayflies *Ephemerella inermis* Eaton and *Baetis tricaudatus* Dodds in the Pembina River, Alberta, Canada. To evaluate the extent to which the organisms are capable of controlling their return to the substrate, I worked with both live and dead animals.

Materials and methods — Experiments were conducted during the last 2 wk of May (spring) and the first 2 wk of October (autumn) 1979, on the Pembina River (53°37′N,

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Printed in Canada (J7312)
Imprimé au Canada (J7312)

115°00′W). The river at the study site is wide (about 65 m) and shallow (maximum depth 1.2 m) during normal flow conditions, with a substrate of smooth cobbles embedded in coarse sand. Macrophytes are absent. Ciborowski and Clifford (1983) provided a detailed description of physical characteristics.

The study site was mapped prior to experiments each season. A base line was established along the south river margin. Water depth and mean current velocity (Ott C-1 current meter at 0.6× depth) were measured at 1-m increments along each of 11 transects, to a distance of at least 12 m from the base line. Linear regression was then used to estimate the relationship between distance from shore and mean current velocity.

Suspended animals were sampled with 12 contiguous drift nets extending from river margin to center. Nets (pore size 0.211 mm) had a mouth opening of 1.0 × 0.5 m and were 2 m long. Each was anchored with aluminum rods driven into the substrate to filter a column of water 1 m wide and up to 0.5 m deep.

Settling rates were determined for animals along each of five lines established parallel to the base line upstream of the nets, at distances of 2, 4, 6, 8, and 10 m from shore. Five wooden stakes were driven into the substrate along each line to serve as insect release points (Table 1).

Large insects (head widths >0.7 mm in spring, 0.4–0.6 mm in autumn, as determined by later laboratory measurements) were hand-collected and kept in finger bowls containing river water until required. Those designated for dead animal trials were preserved in Kahle's fluid to which was added lignen pink dye (10 drops of saturated solution per 15 mL preservative) and transferred to finger bowls containing river water 30 min before use. *Ephemerella inermis* nymphs were too small and cryptic to be used during autumn experiments.

A trial consisted of releasing 50 live and 50 dead animals of each species into the water just above the streambed at a single stake. Animals were released by placing them in a 118 mL jar containing river water, immersing the jar and removing the lid. Drift nets were submersed for 2 min from the time of release. This provided adequate time for animals to be transported from furthest upstream release points to the nets, yet minimized inclusion of detritus and extraneous drifting animals. The contents of each net were separately enumerated in the field.

To estimate numbers of extraneous animals caught during experiments, the nets were used to sample natural drift at 18:00, 24:00, 09:00, and 12:00 on 28–29 May and 7–8 October 1979. Nets were submersed for 2–5 min in spring and 15–25 min in autumn. Sampling period varied to ensure that nets did not become clogged with detritus at higher current velocities. Net contents were preserved in Kahle's fluid and sorted in the laboratory. The estimated mean number of appropriately sized *B. tricaudatus* and *E. inermis* nymphs caught per 2 min in daytime drift samples in each net was used as a correction factor for settling trials.

Instantaneous settling rates (r) of live and dead animals of each species for each experimental line were determined by linear regression according to the formula

$$(1)\quad \ln (n_x + 1) = \ln (n_0 + 1) - rx$$

(McLay 1970; Elliott 1971) where

n_x = number of individuals caught in all nets (corrected for extraneous animals)
n_0 = number released
x = downstream distance between point of release and the nets.

Mean current velocity (v_y) for each line (y m from shore) was estimated from the regression equations relating velocity to distance from shore. The relationship between r and v was then determined by linear regression, following logarithmic transformation of both variables (Elliott 1971; Ciborowski and Corkum 1980). The results were then retransformed to the form

$$(2)\quad r = \beta_1 v^{-\beta_2}$$

where β_1 and β_2 are regression constants.

To compare overall settling capabilities of animals, settling capacity (SC) and behavioral settling index (BI) were calculated (Ciborowski and Corkum 1980). SC is determined by integrating equation 2 over the range of mean current velocities tested (approximately 10–50 $cm \cdot s^{-1}$, Table 1). The relative contribution of behavior (BI) to settling ability is the complement of the ratio of settling capacities of dead to live animals.

Diffusion theory predicts that suspended particles should disperse normally and in proportion to the square root of the distance from their source, along any single axis (Pielou 1969). Turbulence, which is related to current velocity, should contribute an additional diffusion component (Smith 1975). I used multiple regression analysis to estimate how transverse distribution of suspended nymphs varied with downstream distance from the point of release (x) and with mean current velocity (v_y). The dependent variable was the standard deviation (s) of the mean distance from shore of suspended animals caught in nets for each trial. Independent

TABLE 1. Distance from shore (m), mean current velocity ($cm \cdot s^{-1}$) and release points (m upstream of nets) at each line used for settling experiments. Current velocities are interpolated from regression equations in Table 2.

Line No.	1	2	3	4	5
Distance from shore	2	4	6	8	10
Current velocity (spring)	13.9	22.2	30.5	38.8	47.2
Current velocity (autumn)	9.0	18.5	28.1	37.6	36.3
Release points	0.5,1,2,3.5,5	1,2,3.5,5,8	1,2,5,8,11	1,2,5,8,11	1,2,5,9,12

TABLE 2. Regression estimates of relationship between mean current velocity (v_y, cm·s^{-1}) and distance from shore (y, m) at sample site.

Season	Intercept	Slope (SE)	R^2
Spring	5.64	4.151(0.340)	0.77
Autumn	−0.56	4.773(0.285)	0.84

variables were $\sqrt{x}$, and v_y. These regressions took the form

$$(3) \quad s = \beta_3 + \beta_4\sqrt{x} + \beta_5 v_y$$

where β_3, β_4, and β_5 are regression constants.

Results and discussion — Mean current velocity was a linear function of distance from the river margin during both seasons (Table 2), although in autumn velocity became constant at distance from shore greater than 8 m (ANOVA, $P > 0.05$).

Downstream transport — Settling rate was inversely related to current velocity in all series of trials, and live animals exhibited greater settling rates than dead ones (Table 3). In spring, settling rates of *B. tricaudatus* and *E. inermis* nymphs were comparable at low velocities, but *E. inermis* had much lower settling rates at higher mean current velocities than did *B. tricaudatus* nymphs. The different settling rates of live animals were largely due to variations in BI. Although SC due to morphology (i.e. dead animals) was comparable for the two taxa (Table 3), behavior accounted for 0.60−0.64 of total settling capacity for *B. tricaudatus* and only 0.33 of total SC for *E. inermis*. A rapid thigmotactic response to chance contact with the substrate is of primary importance in removing animals of both taxa from the water column (Ulfstrand 1968; Luedke and Brusven 1976; Walton 1978; personal observations), but *Baetis* nymphs are strong swimmers and are better able to control their orientation during transport, especially at higher current velocities (Elliott 1971; McKone 1975). My estimates of BI are somewhat lower than earlier reported determinations for other *Baetis* (0.71−0.82) and *Ephemerella* (0.43−0.62) species (Ciborowski and Corkum 1980).

Lateral transport — Regressions accounted for between 0.49 and 0.79 of total variation in the dependent variable, s (Table 4). All β_4 regression coefficients were significantly greater than zero ($P < 0.01$) and consistently removed more of the variation in s than did β_5; the distance animals were transported downstream was a more important predictive variable than was current velocity. The β_5 coefficients were greater than zero for all analyses except that for *E. inermis* (dead) nymphs.

Relative magnitude of the regression coefficients indicates that dead animals should be less dispersed than live individuals for a given current velocity and distance below a release point. However, because dead animals settle over greater downstream distance than live ones, direct comparison of the coefficients is inappropriate. To provide a better indication of potential lateral dispersal, both between live and dead animals as well as between species, I first determined the estimated distance required for one-half of each sample population to settle ($x_{0.5}$, McLay 1970) where,

$$(4) \quad x_{0.5} = \ln(1/0.50)\, r^{-1} = 0.6931\, r^{-1}$$

I calculated values of $x_{0.5}$ for each species, using values of r corresponding to hypothetical releases of animals made 2 and 10 m from shore. In each case r was interpolated from equation 2, using values of v estimated from spring current velocity regressions (Table 2). These estimates represent how far downstream of the release point animals would be at the time one-half had settled (Table 5). Provided that river width does not vary, the mean distance from shore of the 25 animals still suspended will be the same as it was when they were initially released (y), but they will now be normally distributed with a standard deviation given by equation 3. I constructed frequency histograms for the expected transverse distribution of suspended animals by substituting $x_{0.5}$ and v into equation 3 to obtain expected standard deviations (Table 5) and fitting a normal distribution about y.

Dispersal of suspended animals was much greater along the 10 m line than along the 2 m line (Fig. 1). Live *E. inermis* became more widely dispersed than live *B. tridaudatus* nymphs, but dispersal differences between larger (spring) and smaller (autumn) *B. tricaudatus* nymphs were minimal. Even though $x_{0.5}$ was markedly smaller for live than for dead organisms, there were no consistent trends between transverse dispersal of live and dead individuals of the same species. Clearly, the behavioral mechanisms that reduce downstream transport of live animals have the additional effect of substantially increasing transverse movement.

Lateral dispersal may be more important than animals' downstream transport in a wide, shallow river such as the Pembina. Because longitudinal changes in flow structure

TABLE 3. Regression coefficients (β_1, β_2) and coefficients of determination (R^2) of relationship between instantaneous settling rate (r) and mean current velocity (v) (equations take the form $r = \beta_1 v^{-\beta_2}$), and measures of settling ability (SC, BI).

Species	Condition	β_1	β_2 (SE)	R^2	SC	BI
E. inermis (spring)	Live	33.15	1.65(0.187)	0.96	7.41	0.34
	Dead	18.23	1.59(0.600)	0.70	4.84	
B. tricaudatus (spring)	Live	8.01	1.07(0.116)	0.97	10.38	0.64
	Dead	3.43	1.13(0.402)	0.72	3.69	
B. tricaudatus (autumn)	Live	1.46	0.68(0.084)	0.96	6.42	0.63
	Dead	1.12	0.91(0.267)	0.68	2.38	

TABLE 4. Regression coefficients (β_3, β_4, β_5) of relationship between standard deviation of mean distance from shore of suspended animals (s), distance downstream from point of release (x), and mean current velocity (v). Equations take the form $s = \beta_3 + \beta_4\sqrt{x} + \beta_5 v$. Asterisks indicate regression coefficient significantly greater than zero by ANOVA; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Species	Condition	β_3	β_4 (SE)	β_5 (SE)	R^2
E. inermis (spring)	Live	−1.023	0.600(0.209)**	0.0296(0.0114)**	0.58
	Dead	0.031	0.234(0.068)**	0.0016(0.0036)	0.55
B. tricaudatus (spring)	Live	−0.560	0.659(0.105)***	0.0103(0.0057)*	0.80
	Dead	0.140	0.104(0.025)***	0.0029(0.0014)*	0.56
B. tricaudatus (autumn)	Live	−0.548	0.377(0.111)**	0.0151(0.0073)*	0.48
	Dead	−0.253	0.234(0.056)***	0.0078(0.0041)*	0.60

TABLE 5. Estimates of instantaneous settling rates (r), distance traveled before one-half of animals settle ($x_{0.5}$), and standard deviation (s) of mean distance from shore of suspended animals at $x_{0.5}$.

		Release distance (y)					
		2 m (v_y = 13.9)			10 m (v_y = 47.2)		
Species	Condition	r	$x_{0.5}$	s	r	$x_{0.5}$	s
E. inermis (spring)	Live	0.431	1.61	0.150	0.057	12.07	2.459
	Dead	0.278	2.50	0.423	0.040	17.44	1.084
B. tricaudatus (spring)	Live	0.479	1.45	0.377	0.130	5.35	1.450
	Dead	0.175	3.95	0.387	0.044	15.74	0.689
B. tricaudatus (autumn)	Live	0.244	2.84	0.297	0.106	6.53	1.128
	Dead	0.102	6.79	0.465	0.034	20.65	1.179

occur over distances much in excess of the downstream distance an animal is likely to drift, it is improbable that an individual will be carried from, e.g. a riffle into a pool. In contrast, except at the river center, current velocity changes rapidly across the river. Consequently, settling animals will more likely experience a change in the primary physical factor controlling microhabitat (current velocity) as the result of lateral dispersal than because of downstream movement.

The instantaneous distribution of suspended nymphs is not by itself an accurate measure of the eventual transverse distribution of nymphs in the substrate. As individuals become increasingly widely laterally dispersed, they come under the influence of increasingly different current velocities. Those insects carried laterally to slower water, near shore, will have greater settling rates than those carried away from the shore, where water is faster (equation 1). Thus, although the instantaneous distribution of suspended animals may be normal, the distribution curve of insects that actually do settle at any distance (x) downstream of a release point should be skewed towards the river center, and mean distance from shore should be less than that of the release point (y). The skewness and reduction in mean distance from shore will be governed by how quickly mean current velocity increases with distance from shore (Table 2), and by the rate at which instantaneous settling rate decreases with increasing mean current velocity (equation 1). The latter is largely determined by the behavioral characteristics of the animals. Other physical characteristics of the riverbed such as roughness or presence of macrophytes, which may modify turbulence and settling rate (Elliott 1971), should also influence degree of lateral transport to some extent. Nevertheless, because the exponent of equation 2 is always negative, any animal entering the water column has a greater probability of returning to the substrate closer to shore than of becoming reestablished farther from shore.

If all animals in a population were equally likely to drift, regardless of their initial position in the river, one would expect this population to become concentrated along the river margins, given ample time. However, both *B. tricaudatus* and *E. inermis* nymphs are more prone to enter the drift when in slow water regions than when located in fast water (Ciborowski 1983). This may normally counteract the net effect of lateral transport of suspended animals. Indeed, in the Pembina River, both taxa predominate in fast water away from shore during non-flood conditions (Ciborowski and Clifford 1983). When the river floods, however, animals do become more numerous along the margins. Flooding produces higher current velocities (hence greater downstream and lateral transport) as well as tending to increase the rate of erosion of animals from the substrate through scouring. Lehmkuhl and Anderson (1972) also reported that flooding carried *B. tricaudatus* nymphs to stream margins.

Drift results in a continuous redistribution of animals among lotic microhabitats (Townsend and Hildrew 1976). The microdistribution of populations prone to drift possibly represents the dynamic equilibrium achieved by a balance between departure and settling tendencies of the animals. Prediction of the benthic distribution of nymphs from the drift would require determination of the joint probabilities of departure from the substrate, downstream movement and lateral transport of animals in each microhabitat. However, consideration of the influence of these parameters on micro-

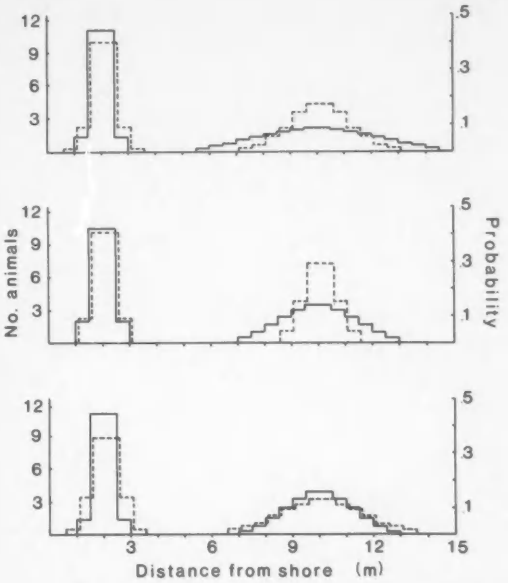

FIG. 1. Hypothetical frequency distribution of suspended animals released 2 and 10 m from shore at the point downstream by which one-half have settled. Left vertical scale indicates animals remaining from an initial release of 50. Right vertical scale represents probability of a suspended animal being a distance from shore indicated by horizontal scale. Top, *E. inermis* (spring); center, *B. tricaudatus* (spring); bottom, *B. tricaudatus* (autumn). Solid lines represent live animals; broken lines represent dead animals.

distribution may provide important insights into the population dynamics of these species.

Acknowledgments — I thank Mr G. Moldenhauer and Dr L. D. Corkum for assistance with the field work. Drs L. D. Corkum, H. F. Clifford, and R. D. Routledge provided critical comments on the manuscript. This research was supported by a grant from the Boreal Institute for Northern Studies, and by an NSERC Canada grant to Dr H. F. Clifford.

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Use of the Size–Frequency (Hynes) Method to Estimate Annual Production of a Stream Fish Population

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GARMAN, G. C., AND T. F. WATERS. 1983. Use of the size–frequency (Hynes) method to estimate annual production of a stream fish population. Can. J. Fish. Aquat. Sci. 40: 2030–2034.

Previously developed and accepted methods of fish production estimation, such as instantaneous growth (G method), require aging of sampled individuals. Hynes' size–frequency method, however, does not require cohort separation. Annual production and approximate 95% confidence intervals are presented and compared for populations of brook, brown, and rainbow trout (*Salvelinus fontinalis, Salmo trutta,* and *Salmo gairdneri*) in Valley Creek, Minnesota, 1977–78, using the size–frequency and G methods. No significant difference was found between production values calculated by the two methods. It is proposed that the size–frequency method provides a reliable determination of annual production of fish populations and will be especially useful where accurate aging of individuals is not possible or where aging represents excessive labor.

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Des méthodes mises au point et acceptées antérieurement pour estimer la production en poisson, telles que celles de la croissance instantanée (méthode G), reposent sur la détermination de l'âge d'individus échantillonnés. La méthode de Hynes, utilisant les fréquences de tailles, ne requiert cependant pas de séparation en cohortes. Nous présentons et comparons dans l'article qui suit la production annuelle et les limites de confiance à 95 % environ de populations d'ombles de fontaine, de truites brunes et de truites arc-en-ciel (*Salvelinus fontinalis, Salmo trutta* et *Salmo gairdneri*) du ruisseau Valley, dans le Minnesota, en 1977–78, à l'aide des deux méthodes, fréquence de tailles et G. Nous n'avons pas détecté de différence significative entre les valeurs de production par l'une ou l'autre méthode. À notre avis, la méthode des fréquences de tailles donne une mesure fiable de la production annuelle des populations de poissons et est particulièrement utile dans les cas où il n'est pas possible de déterminer avec précision l'âge de certains sujets, ou encore quand la détermination de l'âge représente un travail trop considérable.

Received December 14, 1982
Accepted July 27, 1983

Reçu le 14 décembre 1982
Accepté le 27 juillet 1983

SECONDARY production, defined as the total tissue elaborated by a heterotrophic population regardless of the fate of that tissue, is the major pathway of ecosystem energy flow. Estimates of production rates of animal populations in inland waters have been used to measure the effects of resource management and perturbations (Hunt 1978; Brynildson and Mason 1975; Benke et al. 1979; Waters 1982), to assess the trophic ecology of populations (Winterbourn 1974; Neves 1979), and to make comparisons between ecologically different systems (Cooper and Scherer 1967).

Application of production ecology to fishery research is well established (Waters 1977; Bagenal 1978; Gerking 1978). Current methods for estimating fish production rates, however, such as the instantaneous growth (G) method (Ricker 1946; Allen 1949), require sampled individuals to be aged, a potential disadvantage.

The size–frequency method of production estimation, originally proposed by Hynes (1961) and later revised and corrected by Hynes and Coleman (1968), Hamilton (1969), and Benke (1979), has been widely employed for aquatic invertebrates (e.g. Krueger and Martin 1980; Waters and Hokenstrom 1980; Maslin and Pattee 1981). Although used

[1]Cooperators include the U.S. Fish and Wildlife Service, Maine Department of Inland Fisheries and Wildlife, and the University of Maine.

Printed in Canada (J7169)
Imprimé au Canada (J7169)

exclusively with aquatic invertebrates, the method is conceptually applicable to other animals (Waters 1977). Based on the annual summation of individual losses from one size group to the next, the size–frequency method has the advantage in that cohort separation (i.e. aging) is not required. The method, therefore, has potential application to fish populations, particularly where aging poses a problem due to environmental or climatic conditions, lack of suitable structures (e.g. scales, otoliths), or an excessive investment in time and cost required to age many individuals.

In this paper we present explicit formulas for estimation of annual production and its associated variance for fish populations by the size–frequency method and provide an empirical example of the calculations. The accuracy of the method is tested by comparison with the G method.

Formulas — Two sets of data, estimated absolute density of the population (numbers per hectare) ordered by arbitrary length groups and mean individual weights by length group, are required for each date the population is sampled. An estimate of the variance associated with each value is calculated as a measure of sampling variability. The steps involving calculation of fish production rates by the size–frequency method are similar to those presented by Krueger and Martin (1980) for aquatic invertebrates. A major difference, however, involves their treatment of invertebrate mean individual weights as constants, clearly not acceptable with fish.

In equations 1–6, sampling dates are indexed by $i (i = 1,2,\ldots,a)$, giving a total dates, and length groups by $k (k = 1,2,\ldots,c)$ for a total size range of c equal length groups. Indexing follows the notation of Newman and Martin (1983). Parameter $\hat{N}_{ik}$, then, would represent the estimated number of individuals within the kth length group on date i. The values of $\hat{N}_{ik}$ and its variance may be estimated by mark–recapture (Seber 1982), removal (Zippin 1958), or other appropriate method.

The annual mean number of individuals within the kth length group is estimated by

$$(1) \quad \hat{\bar{N}}_{\cdot k} = \frac{\sum_{i=1}^{a-1} (D_{i+1} - D_i) \frac{\hat{N}_{ik} + \hat{N}_{i+1k}}{2}}{D_a - D_1}$$

where $\hat{N}_{ik}$ is the density value for the ith date within the kth length group and D_i is a weighting factor representing the interval, in days, between the ith date and the first sampling date. Weighting is necessary only when the intervals between sampling dates are unequal. The sampling variance (V) of each length group's estimated mean annual density ($\hat{\bar{N}}_{\cdot k}$) is estimated by

$$(2) \quad V(\hat{\bar{N}}_{\cdot k}) = \left\{(D_2 - D_1)^2 \left[\frac{V(\hat{N}_{1k})}{4}\right] + \sum_{i=2}^{a-1} (D_{i+1} - D_{i-1})^2 \left[\frac{V(\hat{N}_{ik})}{4}\right] + (D_a - D_{a-1})^2 \left[\frac{V(\hat{N}_{ak})}{4}\right]\right\} \Big/ (D_a - D_1)^2.$$

Here, $V(\hat{N}_{1k})$ is the sampling variance of the estimated density of the kth length group on the first sampling date, as calculated for the data sets described previously. Equations 1 and 2 are taken from Krueger and Martin (1980).

Also required for production calculations is the annual mean weight of each length group in the population. This can be expressed as

$$(3) \quad \bar{w}_{\cdot k} = \frac{\sum_{i=1}^{a-1} (D_{i+1} - D_i) \frac{\bar{w}_{ik} + \bar{w}_{i+1k}}{2}}{(D_a - D_1)}$$

where $\bar{w}_{ik}$ is the average weight of those individuals within the kth size group on date i. This representation of the annual mean weight of length group k ($\bar{w}_{\cdot k}$) is used to account for possible shifts in condition factor throughout the year.

Because mean weights for fish cannot be measured without error, the variance associated with each value of $\bar{w}_{\cdot k}$ is estimated by

$$(4) \quad V(\bar{w}_{\cdot k}) = \left\{(D_2 - D_1)^2 \left[\frac{V(\bar{w}_{1k})}{4}\right] + \sum_{i=2}^{a-1} (D_{i+1} - D_{i-1})^2 \left[\frac{V(\bar{w}_{ik})}{4}\right] + (D_a - D_{a-1})^2 \left[\frac{V(\bar{w}_{ak})}{4}\right]\right\} \Big/ (D_a - D_1)^2.$$

The size–frequency method was originally proposed for use with univoltine aquatic insects (i.e. one cohort present through the entire year). Benke's (1979) modification refined the method for multivoltine populations by multiplying the production value by 365/CPI, where CPI = cohort production interval in days from the first appearance of the cohort to emergence by the adult form. The CPI is assumed to be a nonrandom variable. The life histories of most aquatic insects allow convenient determination of the CPI, often to within a few days. With fish, however, the CPI is most easily represented by the average maximum age attained (in years) by members of the population, assuming equilibrium between year-classes. Because of the mathematical influence the CPI has on calculations, the accuracy of annual production estimates is strongly related to the reliability of the CPI values used.

Calculation of annual production ($\hat{P}_{s-f}$) by the size–frequency method using the annual mean abundance and weight values derived for each length group by equations 1 and 3, respectively, is estimated by

$$(5) \quad \hat{P}_{s-f} = \left\{\tfrac{1}{2}c\left[\bar{w}_{\cdot 1} (\hat{\bar{N}}_{\cdot 1} - \hat{\bar{N}}_{\cdot 2} + \sum_{k=2}^{c-1} \bar{w}_{\cdot k} (\hat{\bar{N}}_{\cdot k-1} - \hat{\bar{N}}_{\cdot k+1}) + \bar{w}_{\cdot c} (\hat{\bar{N}}_{\cdot c-1} - \hat{\bar{N}}_{\cdot c})\right]\right\}(1/\text{CPI})$$

giving annual production as total losses of tissue from the population over a 12-mo period. Because the use of geometric mean weights (Krueger and Martin 1980) did not result in significantly different values of $\hat{P}_{s-f}$ for the test case, the mean weight values ($\bar{w}_{\cdot k}$) used in equation 5 are arithmetic.

Using the results of equations 2 and 4, the variance of the production estimate due to sampling error is obtained from

TABLE 1. Factors computed by equations 1–4 for three species of trout in Valley Creek, Minnesota, during 1977 and 1978.

Length group	$\hat{\bar{N}}_{\cdot k}$ (numbers·ha^{-1})	$\hat{V}(\bar{N}_{\cdot k})$	$\bar{w}_{\cdot k}$ (g)	$V(\bar{w}_{\cdot k})$
Brook trout				
1	118.4	710.7	2.8	0.2
2	779.4	2394.5	6.8	0.1
3	446.0	533.5	12.3	0.2
4	232.7	126.7	24.4	1.3
5	112.1	20.7	44.0	2.7
6	49.3	78.3	74.1	7.6
7	52.2	981.1	112.9	51.5
8	26.9	27.5	161.3	32.2
9	4.3	0.0	207.8	0.0
Brown trout				
1	197.4	2117.2	2.3	0.1
2	517.7	660.3	5.8	0.1
3	216.5	198.9	12.4	1.0
4	103.9	54.1	25.0	1.5
5	68.1	2.6	44.8	2.1
6	36.6	16.7	74.0	13.5
7	37.5	7.5	109.0	11.4
8	25.9	27.5	174.3	66.5
9	9.2	0.0	221.4	0.0
10	18.2	0.0	280.3	60.5
11	5.5	0.0	328.3	0.0
12	1.8	0.0	350.0	0.0
13	5.5	0.0	521.3	0.0
Rainbow trout				
1	260.2	2653.5	3.2	0.2
2	281.7	1491.4	6.9	0.1
3	144.9	182.5	12.6	0.1
4	88.8	145.9	27.9	1.4
5	67.7	49.5	49.9	5.1
6	43.1	19.5	75.7	45.0
7	55.9	601.4	109.5	24.8
8	26.9	61.2	158.6	11.8
9	19.8	104.2	196.0	39.9
10	15.0	0.2	260.8	13.1

TABLE 2. Annual production and the approximate 95% confidence interval half-length for the production estimate, computed for three species of salmonids in Valley Creek, Minnesota, during the period April 1977–April 1978 by the size–frequency and G methods.[a] Mean annual standing stock ($\bar{B}$) and $P/\bar{B}$ ratios are provided for the size–frequency method only.[b]

Species	Annual production (kg wt weight·ha^{-1}·yr^{-1})	95% confidence interval half-length	$\bar{B}$	$P/\bar{B}$
Brook trout				
Size–frequency	48.8	6.9	37.2	1.31
G method	46.1	8.1		
Brown trout				
Size–frequency	36.9	2.7	35.0	1.05
G method	38.7	3.9		
Rainbow trout				
Size–frequency	32.8	8.6	31.9	1.03
G method	39.1	6.8		

[a]CPI values used for size–frequency calculations were as follows: brook trout, 4 yr; brown trout, 5 yr; rainbow trout, 3 yr.

[b]$\bar{B}$ calculated as $(\hat{\bar{N}}_{\cdot k})\,(\bar{w}_{\cdot k})$.

$$(6)\quad V(\hat{P}_{s-f}) = \left\{(\tfrac{1}{2}c)^2\left[(\bar{w}_{\cdot 1} + \bar{w}_{\cdot 2})^2 V(\hat{N}_{\cdot 1}) + V(\bar{w}_{\cdot 1})\,(\hat{N}_{\cdot 1} - \hat{N}_{\cdot 2})^2 + \sum_{k=2}^{c-1}(\bar{w}_{\cdot k-1} - \bar{w}_{\cdot k+1})^2 V(\hat{N}_{\cdot k}) + V(\bar{w}_{\cdot k})\,(\hat{N}_{\cdot k-1} - \hat{N}_{\cdot k+1})^2 + (\bar{w}_{\cdot c-1} - \bar{w}_{\cdot c})^2 V(\hat{N}_{\cdot c}) + V(\bar{w}_{\cdot c})(\hat{N}_{\cdot c-1} - \hat{N}_{\cdot c})^2\right]\right\}[(1/\mathrm{CPI})^2].$$

In the following example, inclusion of covariance terms in equation 6 slightly reduced $V(\hat{P}_{s-f})$; hence, covariance was treated as zero, giving a slightly conservative overestimate of $V(\hat{P}_{s-f})$. Two standard errors about the annual production estimate can be calculated as

$$(7)\quad \hat{P}_{s-f} \pm 2[V(\hat{P}_{s-f})^{0.5}]$$

giving an approximate 95% confidence interval for the annual production value.

Application and discussion — An empirical example of the size–frequency method is presented for three species of salmonids: brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*) in Valley Creek, Minnesota. Population estimates were made April 1977, September 1977, and April 1978. A description of estimation methods is given by Elwood and Waters (1969). Basic data for fish population estimation are taken from Waters (1983). Absolute density and mean weights of all species were classified by 2.54-cm length increments and annual production was calculated by the size–frequency method using the procedure described previously (Table 1). Where the largest length group of a species included only one individual, the final two length groups were combined and c was reduced accordingly (Waters and Crawford 1973). Annual production and 95% confidence intervals were also computed for all species by the G method of Newman and Martin (1983).

Both methods of production estimation gave results that were not statistically different, based on overlap of approximate 95% confidence intervals (Table 2). The precision of the size–frequency and G method annual production estimates is comparable, as demonstrated by the relative widths of confidence intervals in Table 2. The precision of size–frequency production estimates for aquatic invertebrates may be influenced by the number and size of length classes (Hamilton 1969), sampling regime (Cushman et al. 1978), choice of the CPI (Benke 1979), and the number of sampling dates per year (Benke et al. 1979; Krueger and Martin 1980). The effect of these factors on the reliability of the method's use with fish populations should be investigated further.

Inherent in the size–frequency calculations is the assumption that animals remain in each size group for equivalent periods of time. While the method is robust with respect to violation of this assumption (Menzie 1980), use of nonequal length groups, chosen to reflect age- or size-dependent changes in growth rate, could improve the accuracy of annual production estimates of fish populations by the size–frequency method.

Based on the single empirical test of the form presented here, the size–frequency method appears to provide reliable and accurate estimates of annual production of fish populations. The extensive aging of individual fish required by other methods, such as the G method, is here limited to determination of the population's CPI. Such an advantage will allow investigation of the production ecology of previously problematic fish populations and substantially reduce the time and cost typically associated with fish production calculations. A computer program that calculates annual production rates of fish populations by the size–frequency method is available from the senior author.

Acknowledgments — We are indebted to Raymond Newman for his invaluable assistance with formula derivations. Financial assistance was provided by the Migratory Fish Research Institute of the University of Maine. R. Neves and two anonymous reviewers made valuable comments on the manuscript.

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Cystidicola farionis (Nematoda) as an Indicator of Lake Trout (*Salvelinus namaycush*) of Bering Ancestry

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BLACK, G. A. 1983. *Cystidicola farionis* (Nematoda) as an indicator of lake trout (*Salvelinus namaycush*) of Bering ancestry. Can. J. Fish. Aquat. Sci. 40: 2034–2040.

Cystidicola farionis Fischer is widely distributed in fishes in northern North America west of the Appalachian Mountains. The swimbladders of lake trout (*Salvelinus namaycush*) from 225 localities across North America were examined for the parasite but only those from the Alsek, Coppermine, Flat, Peel, Stikine, Upper Liard, and Yukon River systems were infected with mature nematodes. The ancestors of fishes in these watersheds survived glaciation in a Bering refugium. Thus, this strain of *C. farionis* probably had a refugium in Beringia in the unglaciated parts of the Yukon River system and dispersed from there into northern British Columbia and the coastal mainland of the Northwest Territories during glacial retreat.

BLACK, G. A. 1983. *Cystidicola farionis* (Nematoda) as an indicator of lake trout (*Salvelinus namaycush*) of Bering ancestry. Can. J. Fish. Aquat. Sci. 40: 2034–2040.

Cystidicola farionis Fischer est largement répandu dans les poissons de la partie septentrionale de l'Amérique du Nord, à l'ouest des Appalaches. Les vessies gazeuses de touladis (*Salvelinus namaycush*) de 25 endroits d'Amérique du Nord ont été examinées en vue d'y déceler la présence du parasite, mais seuls les poissons des réseaux Alsek, Coppermine, Flat, Peel, Stikine, Upper Liard et Yukon étaient infestés de nématodes matures. Les ancêtres des touladis de ces bassins ont survécu à la glaciation dans un refuge de Béring. Cette lignée de *C. farionis* avait donc probablement un refuge dans la région de Béring, dans les parties non recouvertes de glaciers du réseau du fleuve Yukon et qui, à partir de là, s'est dispersée dans le nord de la Colombie-Britannique et le long de la côte des Territoires du Nord-Ouest au moment du retrait des glaciers.

Received March 15, 1983
Accepted July 19, 1983

Reçu le 15 mars 1983
Accepté le 19 juillet 1983

CYSTIDICOLA farionis Fischer, 1798 is a parasitic nematode found in the swimbladder of fishes. Thirty-six species of salmonids in nine genera and two species of *Osmerus* may be suitable definitive hosts (Skrjabin et al. 1967; Margolis and Arthur 1979). Several amphipods serve as intermediate hosts including species of *Gammarus*, *Hyallela*, and *Pontoporeia*

Printed in Canada (J7298)
Imprimé au Canada (J7298)

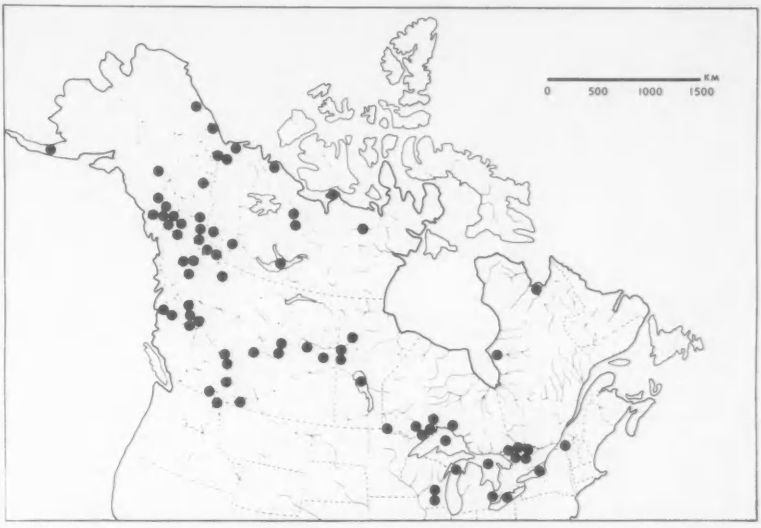

FIG. 1. Distribution of *Cystidicola farionis* in all fishes in North America (sources: Ward and Magath 1917; Skinker 1930; Hunter and Bangham 1933; Smedley 1933; Rawson 1951; Bangham and Adams 1954; Fritts 1959; Anthony 1963; Ko and Anderson 1969; Arthur et al. 1976; Mudry and McCart 1976; Mudry and Anderson 1977; Watson and Dick 1979; Lankester and Smith 1980; Leong and Holmes 1981; this study).

and possibly *Anisogammarus* (Mamaev 1971; Smith and Lankester 1979).

Cystidicola farionis is present in lake trout (*Salvelinus namaycush*) in the Great Lakes, but only immature specimens of the parasite have ever been found in these fish (Lankester and Smith 1980; Black 1983a). In contrast, lake trout in Aishihik Lake, Yukon, commonly harbor large numbers of mature worms (Arthur et al. 1976). These observations suggested that lake trout may not be suitable hosts for *C. farionis* throughout their range. My objective was to reexamine and explain the geographic range over which *C. farionis* matures in lake trout.

Materials and methods — Swimbladders from wild lake trout, Arctic char (*S. alpinus*), and lake whitefish (*Coregonus clupeaformis*) were removed, opened, and visually examined for nematodes. Additionally, preserved specimens of fishes were examined from the following museums: (a) National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario; (b) Royal Ontario Museum, Toronto, Ontario; (c) Muséum de Québec du Loisir de la Chasse et de la Pêche; (d) University of British Columbia Ichthyology Museum, Vancouver, British Columbia; (e) United States National Museum of Natural History, Washington, D.C.; (f) University of Michigan Museum of Zoology, Ann Arbor, Michigan; (g) Cornell University Langmuir Laboratory, Ithaca, New York; (h) University of Manitoba Museum of Zoology, Winnipeg, Manitoba. Almost all fishes were captured during the summer months. To allow access to the swimbladder of museum fishes an incision along the visceral wall was either made or an existing one extended. The bladder was cut longitudinally and its lumen examined. When possible, a maximum of five fish from a particular locality was examined before concluding that the parasite was absent. In addition to these sources, specimens of nematodes from La Grande Rivière, Quebec, were obtained from Paul McKinnis, Institute of Parasitology, Montreal, Quebec. Adult nematodes were identified by examining eggs dissected from the uteri of female parasites (Black 1983a). Immature specimens were examined in *en face* view (Black and Lankester 1980).

Exact counts of parasites in infected fishes were not done although numbers were estimated. A subsample of nematodes was randomly collected from infected fishes from each locality. These worms were distinguished as mature or immature following criteria in Black and Lankester (1981).

Results and discussion — *Cystidicola farionis* is widely distributed in fishes in northern North America west of the Appalachian Mountains (Fig. 1; Table 1). Mature nematodes were found in lake trout from 21 localities[1] on the Alsek, Coppermine, Flat, Peel, Stikine, Teslin, Upper Liard, and White River systems (Fig. 2, 3; Table 1). All lake trout examined were infected in 11 of the 21 lakes and less than 50% in only two (Table 1). Estimated intensity often exceeded 50 worms per fish. The percentage of mature worms in individual fish ranged from 52 to 100%. In contrast, mature *C. farionis* were not recovered from 590 lake trout examined from 204 localities outside of this range (Fig. 2).

[1]Three of six lake trout from Redrock Lake on the Coppermine River that I examined were infected. Ko and Anderson (1969) reported mature *C. farionis* in lake trout here.

TABLE 1. New distributional records of *Cystidicola farionis* in North America.

Location	Host	No. of fish infected/ examined	N	W
Alaska				
Moose Creek	lake whitefish	2/5	62°57′	141°57′
British Columbia				
Dease Lake	lake trout	5/6	58°30′	130°03′
Fraser Lake[a]	mountain whitefish[b]	3/12	54°05′	124°40′
Gladys Lake	lake trout	1/1	57°43′	128°53′
Kidprice Lake[a]	Dolly Varden[b]	14/128	53°56′	127°28′
	rainbow trout[b]	13/44		
Muncho Lake	lake trout	2/3	59°01′	125°47′
Nadina Lakes[a]	mountain whitefish	5/5	53°52′	127°00′
	rainbow trout	34/38		
	sockeye salmon[b]	2/5		
Nanika Lake[a]	Dolly Varden	9/30	53°46′	127°37′
	rainbow trout	3/40		
Simmons Lake	lake trout	2/2	59°10′	129°48′
Stuart Lake[a]	lake trout[c]	1/8	54°30′	124°30′
	lake whitefish	1/5		
	mountain whitefish	1/14		
	rainbow trout	2/31		
Tahtsa Lake[a]	mountain whitefish	3/193	53°40′	127°35′
	rainbow trout	4/143		
Northwest Territories				
Darnley Bay	Arctic char	1/4	69°14′	123°42′
Flat Lakes	lake trout	1/4	62°05′	128°26′
Little Doctor Lake	lake whitefish	1/4	61°53′	123°16′
Macdougall Lake	lake whitefish[d]	—	66°09′	98°35′
Vaillant Lake	lake trout	4/5	66°12′	114°29′
Whitefish Station	Arctic char	1/1	69°44′	132°15′
	lake trout	1/1		
Willow Lake	Arctic char	10/13	68°20′	107°45′
	lake trout[c]	8/14		
Ontario				
Greenwater Lake	lake whitefish[d]	—	48°34′	90°26′
Quebec				
Berthet Lake	lake trout[c]	1/1	58°30′	68°32′
La Grande River	lake whitefish[d]	—	53°50′	79°00′
Lake Champlain	lake whitefish	1/1	45°03′	73°09′
Yukon				
Chadburn Lake	lake trout	6/7	60°39′	134°57′
Dragon Lake	lake trout[c]	2/4	62°36′	131°29′
Finlayson Lake	lake trout	3/5	61°43′	130°30′
Kathleen Lake	lake trout	1/5	60°34′	137°14′
Kluane Lake	lake trout	1/1	61°21′	139°00′
Klukshu Lake	lake trout	1/1	60°19′	137°01′
Louise Lake	lake trout	1/1	60°42′	135°17′
Margaret Lake	lake trout	1/1	65°21′	134°30′
	lake whitefish	3/5		
Quiet Lake	lake trout	3/3	61°05′	133°05′
Simpson Lake	lake trout	1/1	60°44′	129°15′
Stewart Lake	lake trout	2/2	60°38′	128°40′
Teslin Lake	lake trout	1/1	60°13′	132°35′
Toobally Lake	lake trout	3/4	60°17′	126°17′
Watson Lake	lake trout	1/1	60°06′	128°49′

[a]Unpublished data from Dr H. L. Ching (Envirocon Limited, Vancouver, British Columbia).

[b]*Prosopium williamsoni*, *Salvelinus malma*, *Salmo gairdneri*, and *Oncorhynchus nerka*, respectively.

[c]Only immature nematodes recovered.

[d]Prevalence data is unavailable.

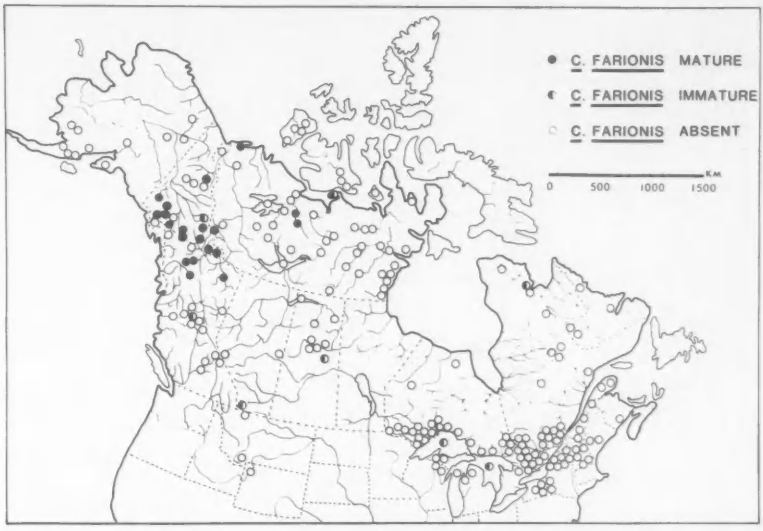

FIG. 2. Localities from which lake trout (*Salvelinus namaycush*) have been examined for *Cystidicola farionis* (see text for additional sources).

Lake trout from a very restricted part of their range harbored mature *C. farionis*. In addition, lake trout from Aishihik Lake on the Alsek River, Yukon are infected with mature *C. farionis* (Arthur et al. 1976). Mature nematodes have not been reported from lake trout by other authors in 59 lakes outside of this area (Hunter and Hunter 1932; Lyster 1940; White and Cable 1942; Bangham and Adams 1954; Bangham 1955; Ko and Anderson 1969; Dechtiar 1972; Hicks and Threlfall 1973; Mudry and Anderson 1977; Lankester and Smith 1980; Leong and Holmes 1981; Stewart and Bernier 1982). Thus *C. farionis* apparently does not mature in lake trout outside of the area shown in Fig. 2 and 3.

The failure of *C. farionis* to mature in lake trout is probably not a seasonal phenomenon. Seasonal studies of the helminth parasites of lake trout in Cold Lake, Alberta, Lake Superior and Greenwater Lake, Ontario have not yielded mature *C. farionis* at any time of year (Lankester and Smith 1980; Black and Lankester 1981; Leong and Holmes 1981). In addition, mature *C. farionis* have been reported in other fishes but not in lake trout examined at similar times of the year in lakes in Alberta, British Columbia, Ontario, and the Northwest Territories (Bangham and Adams 1954; Bangham 1955; Dechtiar 1972; Mudry and Anderson 1977; Lankester and Smith 1980; unpublished data). Similarly, Ko and Anderson (1969) reported *C. farionis* in lake whitefish in several lakes in Algonquin Provincial Park, Ontario, but did not report the parasite in lake trout in those lakes.

The strain of *C. farionis* which matures in lake trout is restricted to areas invaded by fishes which survived the last glaciation in a Bering refugium. Fishes in the Alsek, Peel, Stikine, Teslin, Upper Liard, and White River systems are probably of pure Bering origin (McAllister and Lindsey 1961; Lindsey 1975; Bodaly and Lindsey 1977; Franzin and Clayton 1977; Foote 1979) and those in the Coppermine and Flat rivers and near the Mackenzie River delta are probably hybrids between Bering and other forms (McPhail and Lindsey 1970; Foote 1979). Hence, the data suggest that both host and parasite co-existed in a Bering refugium. The widespread distribution of *C. farionis* in North America suggests that the dispersal of the Bering strain was not restricted by ecological conditions but by the dispersal of its hosts. The distribution of this strain supports the suggestion (Foote 1979) that Bering fishes did not disperse across Western Canada as had been proposed by Franzin and Clayton (1977). Morphometric and meristic characters are in accord with the interpretation that lake trout on Victoria Island and near the Kent Peninsula in the central Arctic are of Mississippi origin (Khan and Qadri 1971; Crossman and McAllister in press). Data on swimbladder nematodes support this finding. A swimbladder nematode of Mississippi origin (*C. stigmatura*) infects lake trout in this region (Black 1983b) whereas the parasite of Bering origin that I considered is apparently absent from the central Arctic.

Within the Bering refugium the strain of *C. farionis* adapted to lake trout probably survived in the unglaciated portion of the Yukon River system. Mixing of fishes from the Yukon and Peel rivers may have occurred when these watersheds were connected by a glacial lake during the last glaciation (Bodaly and Lindsey 1977). Hence, the parasite would have been present in lake trout in Margaret Lake at this time. During deglaciation the headwaters of the Yukon River were connected with the Alsek and Upper Liard rivers allowing dispersal of fish and parasite between these drainage basins (Lindsey 1975; Lindsey et al. 1981). Similarly, temporary lakes and meltwater rivers during deglaciation probably allowed dispersal of organisms from the headwaters of the

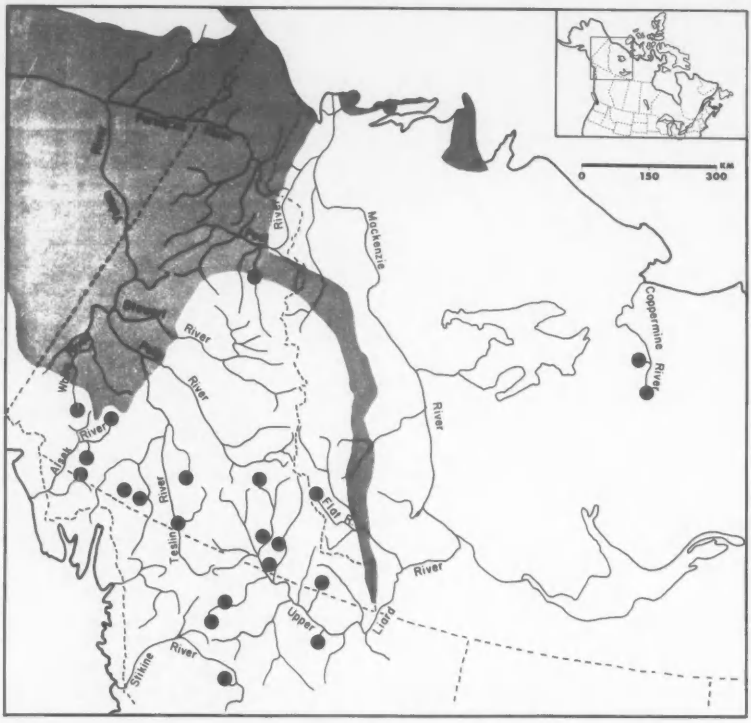

FIG. 3. Proximity of river systems from which lake trout were infected with mature *Cystidicola farionis* (additional source: Arthur et al. 1976). Solid dots represent positive records from lake trout. The shaded area was unglaciated during the last ice age (Prest 1969). Inset: Location of illustrated area in relation to northern North America.

Upper Liard River into the Flat and Stikine rivers. Dispersal of the nematode down the Peel River to the Arctic Ocean probably allowed invasion of coastal areas and the Coppermine River system. More data are required to explain the failure to find the parasite from a few lakes within these watersheds.

Previous confusion in the taxonomy and identification of the species of *Cystidicola* (Black 1983a) has obscured the unusual distribution of *C. farionis* in lake trout. Several reports of *C. stigmatura* (Leidy) in lake trout were misidentified as *C. farionis* (Black 1983a, b). Several other reports should also be reconsidered. Mudry and Anderson (1977) reported *C. farionis* (as *C. stigmatura*) in lake trout in Pyramid Lake, Alberta. The authors did not specify the state of maturity of these nematodes nor are the specimens available for examination. In my study, no mature *C. farionis* was found in four lake trout from Pyramid Lake. Mountain whitefish (*C. williamsoni*) are heavily infected with *C. farionis* in this lake (Mudry and Anderson 1977) and are probably the only suitable host of the parasite there. Ko and Anderson (1969) reported mature *C. farionis* in lake trout from Little Bear Lake, Saskatchewan but I found no mature parasites in 13 lake trout from this lake. Lake whitefish are commonly infected with the nematode in Little Bear Lake (Dr R. C. Anderson, Department of Zoology, University of Guelph, unpublished data) and are probably the usual host in this lake. Ko and Anderson (1969) reported *C. farionis* in lake trout from Takla Lake, British Columbia but did not examine the specimens themselves. Their report requires confirmation since the lake is located outside of the range where the parasite matures in lake trout. Lankester and Smith (1980) reported a few mature *C. farionis* in lake trout in Lake Nipigon. However, the host specificity of the parasite in this lake and Lake Superior is unique. *Cystidicola farionis* is apparently unable to mature in lake whitefish in these lakes (Black and Lankester 1980; Lankester and Smith 1980) while elsewhere they are an important definitive host (see Holmes et al. 1977; Margolis and Arthur 1979; Lankester and Smith 1980). These findings have led to speculation that the swimbladder nematode in Lakes Nipigon and Superior is biologically unique (Black and Lankester 1980; Lankester and Smith 1980). The worm which matures in lake trout in northwestern Canada represents another strain of *C. farionis*. Finally, the report of *C. farionis* in the intestine of one of 156 lake trout in Wyoming (Bangham

1951) is probably a misidentification.

Acknowledgments — I am grateful to the following people for giving me permission to examine museum specimens and for assistance during examinations: D. E. McAllister and B. W. Coad, National Museums of Canada, E. J. Crossman and M. Waters, Royal Ontario Museum, G. Roy, Muséum du Québec, C. C. Lindsey, N. J. Wilimovsky, and R. Carveth, University of British Columbia, B. B. Collette, United States National Museum, R. R. Miller, G. R. Smith, and L. Creighton, University of Michigan, R. Schoknecht, Cornell University, K. Stewart, University of Manitoba. J. W. Clayton and D. Tretiak kindly gave permission to examine and assisted during examinations of lake trout housed at the Freshwater Institute, Winnipeg, Manitoba. In addition, I gratefully acknowledge the collection of specimens by R. J. Cawthorn, T. Johnson, J. C. Underhill, P. E. Ihssen, M. Ackerman, N. Alfonso, V. B. Collins, C. Daigle, J. Durbin, J. L. Fitchett, M. Hanson, D. Perron, A. Sippel, G. M. Stassen, M. L. Villemure, and P. Waring. I thank H. L. Ching, M. W. Lankester, G. Rogers, and L. Stanfield for providing access to unpublished data and G. Himberg for assistance in determining the location of capture of museum specimens of fish.

R. C. Anderson, E. L. Bousfield, D. E. McAllister, and C. Bartlett provided valuable comments on an earlier draft. The work was supported by an NSERC operating grant and Canadian National Sportsmen Show Award to R. C. Anderson, and an Ontario Graduate Scholarship and an NSERC Postgraduate Scholarship to the author.

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Increased Survival in Salmonid Hybrids by Induced Triploidy

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SCHEERER, P. D., AND G. H. THORGAARD. 1983. Increased survival in salmonid hybrids by induced triploidy. Can. J. Fish. Aquat. Sci. 40: 2040–2044.

All possible hybrid crosses between brook (*Salvelinus fontinalis*), brown (*Salmo trutta*), and rainbow (*Salmo gairdneri*) trout were made and a portion of the fertilized eggs from each mating were heat shocked to induce triploidy. Within a species, triploids generally showed poorer survival to the initiation of feeding than diploids. In most crosses, however, triploid hybrids showed much better survival than diploid hybrids. The triploid tiger trout (brown × brook) hybrid showed the most potential of the hybrids tested. Induced triploidy could be a useful general method for increasing survival in interspecific fish hybrids.

SCHEERER, P. D., AND G. H. THORGAARD. 1983. Increased survival in salmonid hybrids by induced triploidy. Can. J. Fish. Aquat. Sci. 40: 2040–2044.

Nous avons réalisé tous les croisements hybrides possibles entre l'omble de fontaine (*Salvelinus fontinalis*), la truite brune (*Salmo trutta*) et la truite arc-en-ciel (*Salmo gairdneri*), et soumis à un choc thermique les oeufs fécondés de chaque croisement dans le but de provoquer la triploïdie. Au sein d'une espèce, les triploïdes ont ordinairement une survie au stade de début de l'alimentation moindre que celle des diploïdes. Dans la plupart des croisements, cependant, les hybrides triploïdes montrent une meilleure survie que les hybrides diploïdes. L'hybride triploïde truite tigre (truite brune × omble de fontaine) est, de tous les hybrides testés, celui qui est le plus prometteur. La triploïdie provoquée pourrait être une méthode utile pour améliorer la survie d'hybrides interspécifiques de poissons.

Received April 19, 1983
Accepted July 18, 1983

Reçu le 19 avril 1983
Accepté le 18 juillet 1983

INTERSPECIFIC fish hybrids show considerable potential for use in fisheries management and fish culture (Harrison 1961; Nelson et al. 1965; Ware 1975; Weithman and Anderson 1977; Chevassus 1979; Laarman 1979; Fraser 1980; Tave et al. 1981). Fish hybrids may show improved growth, may combine the desirable characteristics of two distinct species, and may sometimes be sterile, allowing the manager to control reproduction. However, interspecific hybrids frequently show reduced viability.

Induced triploidy may increase the viability of interspecific

Printed in Canada (J7328)
Imprimé au Canada (J7328)

hybrids. Studies with amphibians (Bogart 1980; Elinson and Briedis 1981) and fish (Capanna et al. 1974; Vasil'ev et al. 1975; Marian and Krasznai 1978; Allen and Stanley 1981, 1983; Sutton et al. 1981; Beck and Biggers 1982; Chevassus et al. 1983) suggest that triploid interspecific hybrids may survive better than diploid hybrids. Triploidy can be readily induced in fish when eggs are treated shortly after fertilization using thermal shocks (Purdom 1972; Valenti 1975; Chourrout 1980; Thorgaard et al. 1981; Wolters et al. 1981; Chourrout and Quillet 1982) or hydrostatic pressure (Yamazaki 1983).

We have compared survival to the initiation of feeding in diploid and induced triploid hybrids among the brook (*Salvelinus fontinalis*), brown (*Salmo trutta*), and rainbow (*Salmo gairdneri*) trout. Triploid hybrids generally showed increased survival; induced triploidy may prove useful for producing more vigorous interspecific salmonid hybrids.

Materials and methods — Brook and brown trout eggs and sperm were obtained from the Ford Hatchery of the Washington Department of Game. Rainbow trout eggs and sperm were obtained from the Spokane Trout Hatchery of the Washington Department of Game. After transporting the eggs and sperm to Washington State University on ice, three single-pair matings of all possible crosses were attempted. The eggs were fertilized in dechlorinated tap water, and 10 min after fertilization a portion of each pair-mating was heat shocked by immersion in a 28°C water bath for 10 min (Chourrout 1980). The eggs were then cooled in a bath of 10°C dechlorinated tap water and placed in a 10°C recirculating incubation system.

The fertilized eggs from the three single-pair matings for each experimental cross were kept separate during incubation to note variations in egg condition, susceptibility of the eggs to the heat shock treatment, and survival. Dead (white) eggs and fry were carefully removed several times weekly beginning 11–12 d after fertilization. One brown trout female (BT_3) apparently had poor egg quality (less than 40% survival in the control cross at the eyed stage (Blanc and Chevassus 1979)); all data from crosses involving this female were excluded in estimating relative survival of diploids and triploids.

Chromosome preparations were made from a sample of 14- to 18-d-old embryos (Thorgaard et al. 1981). Counts of chromosomes from five metaphase spreads per individual in the control and suspected triploid lots were used to determine the ploidy of each experimental lot. Diploid hybrid trout have a karyotype representing the sum of the haploid sets of both species. Triploid hybrids have a karyotype representing the sum of the haploid male set and the diploid female set. Diploid chromosome numbers are 80, 84, and approximately 60 in the brown, brook, and rainbow trout, respectively.

Results — Induction of triploidy using the heat shock treatment appeared to be 100% effective in all crosses involving female brook and brown trout (Tables 1 and 2). Crosses involving female rainbow trout showed varying proportions of triploid progeny (Table 3). A possible explanation for the higher percentage of induced triploidy we observed in brook and brown trout eggs is that their smaller egg size and higher surface area to volume ratio permitted more rapid and complete heating and cooling.

TABLE 1. Percent survival and proportion triploidy in crosses involving female brown trout.

Cross[a] (♀ × ♂)	Proportion triploid karyotypes	Number of eggs	Percent survival[c]		
			Day 20	Day 41	Day 58
$BT_1 \times BT_4$					
Heat shock	10/10	106	75.7	34.0	16.0
Control	0/3	87	97.3	67.6	45.9
$BT_2 \times BT_5$					
Heat Shock	8/8	84	75.0	44.0	35.7
Control	0/5	98	87.8	46.9	36.7
$BT_3 \times BT_6$					
Heat shock	4/4	110	30.0	0.0	0.0
Control	0/3	119	37.8	0.0	0.0
$BT_1 \times ST_4$					
Heat shock	10/10	226	65.0	24.3	23.0
Control	0/3	178	83.1	25.8	10.7
$BT_2 \times ST_5$					
Heat shock	10/10	148	83.1	38.5	35.8
Control	0/5	159	83.0	16.4	8.8
$BT_3 \times ST_6$					
Heat shock	7/7	223	14.8	0.0	0.0
Control	0/3	261	15.3	0.0	0.0
$BT_1 \times RT_1$					
Heat shock	—[b]	275	74.9	0.0	0.0
Control	0/3	142	88.0	0.0	0.0
$BT_2 \times RT_2$					
Heat shock	9/9	142	54.9	0.0	0.0
Control	0/3	72	5.6	0.0	0.0
$BT_3 \times RT_3$					
Heat shock	—	183	26.2	0.0	0.0
Control	0/3	233	8.6	0.0	0.0

[a]BT = *Salmo trutta*; RT = *Salmo gairdneri*; ST = *Salvelinus fontinalis*.

[b]— = no chromosome spreads obtained.

[c]The three days listed correspond to the approximate times of appearance of eye pigment, hatching, and initiation of feeding.

Hybridizations involving female brown trout — The diploid within-species brown trout lots showed better survival to the initiation of feeding than the triploid lots (Table 1). This advantage is largely due to the higher initial survival at the eyed state (approximately day 20) in the diploid lots. The relatively high survival of triploids in one lot ($BT_2 \times BT_5$) suggests that the heat shock treatment, rather than triploidy per se, may be responsible for most of the initial reduction in survival.

In the brown × brook trout hybrid, however, the triploid lots survived better than the diploid lots to the initiation of feeding (Table 1). Survival of triploid tiger trout, relative to the diploid intraspecific lots involving the same female, averaged 73.8%. This was a much higher relative survival than we found in diploid hybrids (23.7%), and approximately the same as the triploid brown trout lots (66.1%).

In hybridizations to rainbow trout males, none of the eggs in either the diploid or triploid lots survived to hatching. Our results are consistent with other published results of attempted hybridizations involving rainbow trout males and brook or brown trout females (Buss and Wright 1956; Suzuki and Fukuda 1971a; Refstie and Gjedrem 1975; Blanc and Chevassus 1979). It has been suggested that the poor success

TABLE 2. Percent survival and proportion triploidy in crosses involving female brook trout.

Cross[a] (♀ × ♂)	Proportion triploid karyotypes	Number of eggs	Percent survival[c] Day 20	Day 45	Day 67
$ST_1 \times ST_4$					
Heat shock	10/10	175	91.4	74.9	60.6
Control	0/3	170	98.8	94.7	85.3
$ST_2 \times ST_5$					
Heat shock	10/10	196	9.2	5.6	5.6
Control	0/3	122	63.1	52.5	46.7
$ST_3 \times ST_6$					
Heat shock	10/10	216	88.9	67.1	51.4
Control	0/3	144	97.2	91.7	76.4
$ST_1 \times BT_4$					
Heat shock	10/10	375	65.1	9.9	6.1
Control	0/3	282	37.6	0.0	0.0
$ST_2 \times BT_5$					
Heat shock	—[b]	343	19.0	0.3	0.3
Control	—	219	26.0	0.0	0.0
$ST_3 \times BT_6$					
Heat shock	10/10	412	62.9	25.5	18.7
Control	0/3	310	89.4	3.5	0.0
$ST_1 \times RT_1$					
Heat shock	—	442	24.0	0.2	0.2
Control	—	290	25.5	0.0	0.0
$ST_2 \times RT_2$					
Heat shock	—	323	17.0	1.2	0.0
Control	—	254	17.3	6.3	0.0
$ST_3 \times RT_3$					
Heat shock	10/10	288	78.1	0.3	0.0
Control	0/3	347	94.5	0.0	0.0

[a]ST = *Salvelinus fontinalis*; BT = *Salmo trutta*; RT = *Salmo gairdneri*.

[b]— = no chromosome spreads obtained.

[c]The three days listed correspond to the approximate times of appearance of eye pigment, hatching, and initiation of feeding.

TABLE 3. Percent survival and proportion triploidy in crosses involving female rainbow trout.

Cross[a] (♀ × ♂)	Proportion triploid karyotypes	Number of eggs	Percent survival[b] Day 18	Day 31	Day 53
$RT_4 \times RT_7$					
Heat shock	6/10	93	78.5	44.1	16.1
Control	0/3	65	100.0	90.8	89.2
$RT_5 \times RT_8$					
Heat shock	10/10	158	100.0	98.7	96.8
Control	0/3	119	100.0	96.6	94.1
$RT_6 \times RT_9$					
Heat shock	0/10	86	93.0	76.7	52.3
Control	0/3	66	85.7	78.6	69.6
$RT_4 \times ST_7$					
Heat shock	5/7	106	89.6	54.7	9.4
Control	0/3	116	89.7	63.8	0.0
$RT_5 \times ST_8$					
Heat shock	10/10	170	98.2	96.5	7.1
Control	0/3	164	99.4	90.2	0.0
$RT_6 \times ST_9$					
Heat shock	0/10	158	86.7	70.9	5.7
Control	0/3	160	96.3	83.8	13.8
$RT_4 \times BT_7$					
Heat shock	6/8	175	76.0	32.0	3.4
Control	0/3	158	96.2	73.4	0.0
$RT_5 \times BT_8$					
Heat shock	10/10	235	100.0	89.4	67.7
Control	0/3	190	96.3	78.4	0.0
$RT_6 \times BT_9$					
Heat shock	0/10	145	84.1	46.2	0.0
Control	0/3	170	95.3	71.8	0.0

[a]RT = *Salmo gairdneri*; ST = *Salvelinus fontinalis*; BT = *Salmo trutta*.

[b]The three days listed correspond to the approximate times of appearance of eye pigment, hatching, and initiation of feeding.

rate in hybridizations involving these species is a result of differences in egg-incubation time causing a disruption of normal embryonic development (Buss and Wright 1956).

Hybridizations involving female brook trout — The brook trout diploid controls showed better survival than the triploid lots in all instances (Table 2). Conversely, the triploid brook × brown trout hybrids showed better survival than the diploid hybrids. None of the diploid hybrids survived to the initiation of feeding. Suzuki and Fukuda (1971b) found only 0.3% survival in this diploid hybrid to age 1. However, some of our triploid hybrids survived to the initiation of feeding (mean relative survival = 10.8%). The triploid intraspecific lots (mean relative survival = 50.1%) survived much better than the triploid hybrids.

The brook × rainbow trout hybrids, like the brown × rainbow trout hybrids, showed poor survival in both the diploid and triploid lots. None of the diploids and only 2 out of over 1000 suspected triploid individuals survived to the initiation of feeding.

Hybridizations involving female rainbow trout — The results from the rainbow trout females were not averaged because of incomplete induction of triploidy in two of three heat-shocked lots (Table 3). Recent experiments suggest that 29°C heat shocks are more effective for inducing triploidy in rainbow trout eggs. In the within-species cross where the heat shock treatment was 100% effective in inducing triploidy ($RT_5 \times RT_8$), the diploid and triploid lots both showed high survival (94.1 and 96.8%, respectively).

In the rainbow × brown trout hybridizations the triploids survived better than the diploids. None of the diploids survived to the initiation of feeding and few eggs hatched. The 100% triploid hybrid lot ($RT_5 \times BT_8$) showed high survival (67.7%) but also a high incidence of curved spines (25%) in the alevins. Deformities were also noted in the 75% triploid lot ($RT_4 \times BT_7$). Chevassus et al. (1983) also observed increased survival of triploid rainbow × brown trout hybrids.

In the rainbow × brook trout hybridization, survival to the initiation of feeding in the 100% triploid lot ($RT_5 \times ST_8$) was low (7.1%) but higher than in the diploid hybrid lot (0%). The 70% triploid lot ($RT_4 \times ST_7$) also showed higher survival than the corresponding diploid lot. Chevassus et al. (1983) observed high survival to 161 d after fertilization in triploid rainbow × brook trout hybrids. The surprisingly high survival we observed in one diploid hybrid lot ($RT_6 \times ST_9$) might be related to differences in developmental rate between eggs from different rainbow trout. Blanc and Chevassus (1979) and

Blanc and Poisson (1983) also noted differences in survival among single-pair matings of salmonid hybrids.

Discussion — Induced triploidy may be a good general method for increasing the survival of fish hybrids. Although our diploid within-species controls in trout survived better than their triploid counterparts to the initiation of feeding, triploid hybrids generally showed much better survival than diploid hybrids. Similar observations of increased triploid viability have been made in other interspecific fish hybrids (references in Introduction). Elinson and Briedis (1981) have speculated that the presence of two maternal chromosome sets allows triploid hybrid amphibian embryos to avoid developmental blocks by producing sufficient quantities of essential molecules.

Tiger trout (brown × brook trout hybrids) showed the most promise of the hybrids we tested. The diploid hybrids have been widely studied (e.g. Harrison 1961; Suzuki and Fukuda 1971a, b, 1973; Blanc and Chevassus 1979, 1982; Blanc and Poisson 1983); they are sterile and show good growth rates. Because of their sterility, female tiger trout have a low proportion of their total body weight in viscera (Suzuki and Fukuda 1973). Induced triploidy could make large scale production of potentially desirable hybrids with reduced survival (such as the tiger trout) feasible.

In addition to increasing survival, induced triploidy may insure sterility of the hybrid. Triploid trout appear to be sterile (Thorgaard and Gall 1979) and thus potentially can avoid the growth depression and survival losses associated with sexual maturation in normal fish. In crosses producing fertile diploid hybrids, triploid sterility may thus improve growth and survival and allow control of reproduction. In crosses with sterile diploid hybrids (such as the tiger trout) control of reproduction can be assured even if induction of triploidy is not 100% effective.

Acknowledgments — We thank Bob Johns, Mike Albert, and the Washington Department of Game for furnishing the trout eggs and sperm. This project was funded by National Science Foundation grant PCM 8108787.

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PERSPECTIVES

Epigenetic Mechanisms: Reflections on Evolutionary Processes

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BALON, E. K. 1983. Epigenetic mechanisms: reflections on evolutionary processes. Can. J. Fish. Aquat. Sci. 40: 2045–2058.

Evolutionary trends leading to certain patterns call for reflection on possible processes which maintain the stability of these patterns and facilitate their changes. Epigenetic processes (like heterochrony) operate mainly in early ontogeny and trigger a chain reaction of changes in induction, regulation and control of the formation of vital structures and functions. Genetic variation maintained by reproduction via supernumerous despecialized zygotes is enhanced by epigenesis. The tendency to optimize, especially in stable and competitive environments, is resisted by a barrier against easy inheritance of selected phenotypic characters, and by juvenilization. If optimization would be allowed to succeed, any new unpredictable perturbation would cause extinction; therefore variations must constantly oscillate around two steady states needed to address any survival goal. This oscillatory process is explained, and named, the Chen principle. The generalist's homeostatic state can be termed altricial and the specialist's precocial. Consequently, "altricial ⇌ precocial dynamic states" form a dichotomy reflected in most evolutionary patterns. Both theories explain the processes we came to perceive as a result of partly closed thermodynamic systems within the open-ended system of nonequilibrium thermodynamics.

BALON, E. K. 1983. Epigenetic mechanisms: reflections on evolutionary processes. Can. J. Fish. Aquat. Sci. 40: 2045–2058.

Devant les tendances évolutives aboutissant à certaines caractéristiques, il est bon de s'arrêter aux processus qui assurent la stabilité de ces caractéristiques et qui facilitent leurs changements. Les processus épigénétiques (tels que l'hétérochronie) agissent en grande partie au début de l'ontogénie et déclenchent une réaction en chaîne de changements d'induction, de régulation et de contrôle de la formation de fonctions et de structures vitales. L'épigénèse peut accentuer une variation génétique maintenue par la reproduction via d'innombrables zygotes ayant perdu leur caractère spécialisé. Cette tendance à l'optimisation, surtout dans des environnements stables et compétitifs, est freinée par une barrière à la transmission héréditaire facile de caractères phénotypiques choisis et par rajeunissement. Si l'optimisation pouvait réussir en toute liberté, une perturbation nouvelle imprévue, quelle qu'elle soit, entraînerait l'extinction; c'est pourquoi les variations doivent osciller constamment entre deux états d'équilibre nécessaires à la survie. Nous expliquons ce processus oscillatoire, que nous appelons principe de Chen. L'état homéostatique du généraliste peut être qualifié de nidicole et celui du spécialiste, de nidifuge. Comme conséquence, les « états nidicoles ⇌ nidifuges dynamiques » forment une dichotomie qui se reflète dans la plupart des schémas évolutifs. Les deux théories expliquent les processus qu'on perçoit maintenant comme le résultat de systèmes thermodynamiques clos à l'intérieur du système libre de thermodynamique de non-équilibre.

Received January 18, 1983
Accepted July 21, 1983

Reçu le 18 janvier 1983
Accepté le 21 juillet 1983

Learning leads to the overpacked mind.
By return to the unlearned and mass-produced
egg, the ongoing species again and again
clears its memory banks to be ready
for the new.
GREGORY BATESON (1979)
in *Mind and Nature*

Seven years ago two Perspectives in this journal were devoted to reviews and syntheses of patterns formed by reproductive styles and life histories of fishes (Balon 1975a, b, 1976). In recapitulating these recently in view of evolutionary trends leading to such patterns (Balon 1981b, 1983b), it appeared timely to reflect on the possible processes which maintain the stability of these patterns and facilitate changes from one pattern to another. Unfortunately many mechanisms of epigenesis (Løvtrup 1974) are incompletely understood at the present time and many more not yet correctly interpreted, which considerably decreases the number of convincing examples. Nevertheless, I hope at least to release the

Printed in Canada (J7204)
Imprimé au Canada (J7204)

epigenetic processes from the black box in which some tend to confine them (Dawkins 1982, p. 22). In so doing I intend to show that the epigenetic processes, by reacting to environmental cues, do not only trip the switches of the genetic programs on and off. I believe we can now do better than replace Wolff's *vis essentialis* (Roe 1979) by gene-replicators (Dawkins 1976, 1978).

Incidentally, *epigenesis* in my usage means the interaction of developmental elements leading to the construction of a phenotype (includes the rare reverse-transcriptions across the genetic barrier); *genetic* describes the dynamic state of elements in the replicating line, the genome (various types of genes, replicators, e.g. split genes, multigene clusters, etc.) and *epigenetic* describes the interactions among gene products, cells, tissues, organs, and the environment in the formation of an organism.

In a most simple way my theme can be introduced, hesitantly, by the following example Richard Dawkins recently used (in a seminar at our University) to explain the action of modifier genes: Let us imagine an irregular sheet — representing a phenotype — hanging from the ceiling on rubber bands of various lengths. The shape of the sheet depends both on the position of the upper (gene) to lower (phenotypic effects) attachment points and the various tensions exerted on one band by the other bands at their crossing-touching points (modifiers).

This picture lends itself well to be extended for my view of life: In addition to the Dawkinsian perception, the shape of the suspended sheet depends also on, for example, the age, structure, and condition of the rubber, a wind blowing against the rubber bands from one side (environment) and on the amount of rubber dissolving particles the wind carries and which interact with the rubber (epigenesis). In the latter case some rubber bands, especially at the upwind side, will break, affecting severely the shape of the sheet (phenotype). The purpose of respective attachment points is at the same time eliminated. If addition of other bands instead of the dissolved bands by some kind of whirlpool winds could be imagined (a difficult thing indeed), a case for reverse transcriptions may be made and the picture completed. With all the limitations of such an example, it again illustrates that the older story is not incorrect, but merely incomplete.

The recent proliferation of literature pertinent to epigenesis is such that I cannot possibly survey, read and integrate it all. In order to prepare the background for the recapitulation (Balon 1983b), I discovered works, missed earlier or published since, addressing similar phenomena and arriving at similar conclusions (e.g. Bateson 1979; Alberch 1980; Rosen and Buth 1980; Vrba 1980; Stearns 1980; Schopf 1981a, b; Oppenheim 1981; Wiley and Brooks 1982; Gould 1982a, b). No better is this evident than from the Report of the Dahlem Workshop on Evolution and Development, Berlin, 1981, May 10–15 (Bonner 1982), unfortunately received only after a number of revisions of this paper had been completed; the need of yet another revision and integration, I rationalize, would serve no purpose but make this review a little more complete in an over-reviewed field at any rate. The conclusions reached at Dahlem collectively, although based mostly on an entirely different set of sources to mine, conform so closely with my views, as expressed earlier (Balon 1979a, b; 1981a) and presented here, that their convergent evolution, it be the case, is almost unbelievable. Much the same applies to many statements made and views expressed by Løvtrup (1982a, b, c, d, e). In one way this is encouraging, for when similar conclusions are reached by different minds using diverse organisms and points of view, the resultant theories must be more convincing, but in another way this is discouraging, for one's confidence is shattered in being neither first nor original.

Each evolutionary pattern loses some realism with every step towards generalizations. It is useful to, sort of, descend from the holistic tower, right "through the looking-glass." Frankly, I cannot resist this metaphor for several reasons: The year I first presented (CCFFR, Ottawa, January 1982) and wrote this marks both the 150th anniversary of the birth of Charles Dodgson and the 100th anniversary of the death of Charles Darwin. Darwin's (1859) writing destroyed for many the comfortable belief in natural order. Dodgson was quick to grasp and react. I find, therefore, over and over again (Balon 1975b, 1976) much ultimate meaning in Alice's adventures, of which at least two reflect the central theses of this paper. The "Chen Principle," formulated in this paper, may explain why "The creatures she meets will always go round and round their mad tea tables and pointless caucus rings, with no possible rationale or goal, no final end to their circles — graphic metaphors for the Darwinian model of nature's (. . .) endless round of self-preservation . . ." (Rackin 1982); and the ability to escape specialization through reproduction and paedomorphosis resembles ". . . living backwards . . . always makes one a little giddy at first . . . but there's one great advantage in it, that one's memory works both ways" (Carroll 1871).

Variation, Saltation, and Heterochrony

Apparently there are at least two sources (e.g. Templeton 1982) of significant variation upon which selection acts; some scientists believe in one or the other source only, and other doubt any such source. (I shall leave others to integrate S. Wright's (1980) theory of shifting balance evolution with this, if applicable.) The first source is genetic variation, maintained and enhanced by random mutations (see Schopf 1981a). Some claim this to be the only source of variation available for natural selection. "Genes are allowed to exert their normal effect on development. Their developmental consequences — phenotypic effects — feed back on those genes' chances of surviving, and as a result gene frequencies change in succeeding generations in adaptive direction" (Dawkins 1982, p. 176). Presumably if selection continues in favor of a certain trend the original variation "will have become used up" (p. 21), in other words, "evolution by natural selection destroys the genetic variance on which it feeds" (Lewontin 1979). Although I do not dispute this "central theme," provided that it is suitably expanded (e.g. Waddington 1961; Medawar 1967; Cohen 1977), the second source of variation (epigenesis) is to me equally important. In contrast to the first source it is mainly nonrandom.

The genome creates the organism for which it is programmed through "a set of instructions which, if faithfully obeyed in the right order and under the right conditions, will result in a body" (Dawkins 1982, p. 175). This "faithful" obedience, however, is not the only way, because "epigenesis

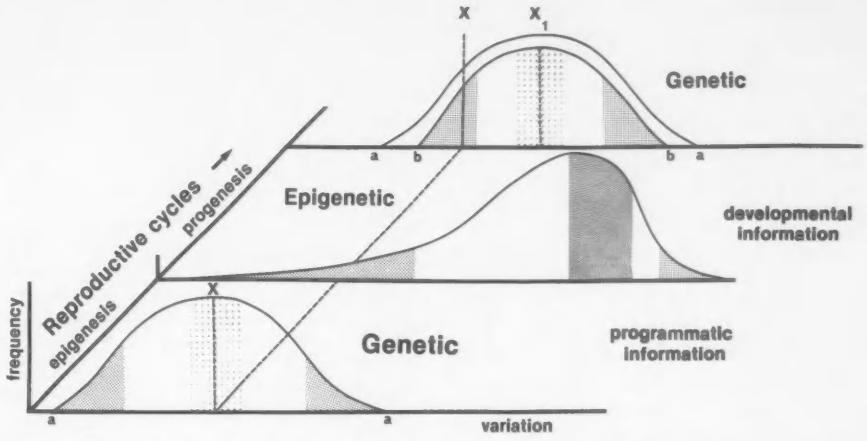

FIG. 1. A hypothetical comparison of the two sources of variation — random genetic and directional epigenetic — under the influence of selectional forces (results of hard selection = dots, results of stabilizing selection = arrowheads, of directional selection = line shaded; $x-x_1$ = effects of reverse transcriptions and genetic assimilations, a−b = used up genetic variation; the time axis uses Løvtrup's (1974, p. 397) concept of a reproductive cycle as a hypothetical multi-generational scale, where progenesis = the germ line phase, epigenesis = the phase of a parent phenotype).

is not a process which is programmed in detail, but rather, like a computer operation, prevails in the form of a set of data and some operational instruction, ... small variations in the data (embryogenetic substrate, including the genome) or in the operational instructions (embryogenetic mechanisms) may change the course of the whole operation, and so will interference from the environment" (Løvtrup 1974, p. 401). The implications (see also, e.g. Spemann and Mangold 1924; Rappaport 1975; Papageogiou 1980; Oppenheim 1981; Katz et al. 1981; Cooke 1982), with apology for more quotations, are obvious: "... embryonic development consists of a long series of successive transformations, of which the antecedent ones act as immediate causes of the subsequent ones; each of them, in a certain sense, creates something new and provokes, in the same stroke, the activity of factors which up to then had had no occasion to intervene" (Brachet 1921 as translated by Løvtrup 1974, p. 401). The possible mechanisms are many (e.g. Katz and Lasek 1978; Odell et al. 1981), involving "... direct exchange of metabolic products and/or electrical coupling via specialized junctional complexes (...). There are many other ways in which one population of cells may influence (...) a second population during the life of an organism: embryonic inductive interactions, synaptic transmissions, endocrine activity, etc." (Maderson 1975, p. 316).

Both sources of variation are limited and complement each other. The first source, represented by the genome, tends to maintain stable sets of variations (data) and instructions (i.e. information, e.g. in the sense of Wiley and Brooks 1982) in order to reproduce itself most faithfully (see Kryzhanovsky 1968 for a less conventional support). If this programmatic variation becomes depleted and resulting instructions permit less flexibility (plasticity) than required for survival in a given environment and association, extinction is inevitable. This first source is conservative, whereas the second source is liberal. The latter responds freely to environmental cues, reflects the complex dynamic of tissue interactions, and increases variation in the required direction (see review by Alberch 1980). This epigenetic source of variation, in a metaphorical sense, tends to "disobey" instructions at least as often as to obey them as if fighting the restrictions of the first source (genome) and extending the variation in a desired direction (Fig. 1). It is, however, also restricted: "If variations beyond the stated limits occur, most likely the epigenetic processes will go astray, resulting in ontogenetic failure" (Løvtrup 1974, p. 425). In this sense, my metaphor of "disobedience" — a reaction to the textbook orthodoxy — is intentionally exaggerated (from flexibility) and signifies the ability of epigenetic processes to create an alternative to the exact copy desired by the replicator. The exaggeration merely emphasizes my thoughts and is not meant to belittle the interrelationships and dependence of genetic and epigenetic mechanisms (see also Goldschmidt 1940). After all evolution is achieved, if the epigenetic variation, formed repeatedly in a certain direction, is selected and incorporated into the replicators. Therefore, separation of these two sources of variation here serves only a heuristic purpose, for they may not exist as separate entities.

What I object to in the orthodox infatuation with genes (e.g. Dawkins 1976, 1982) is that genes (replicators) are supposed to account for everything in their phenotypes (extended or not) and nothing else matters. It seems to me highly unlikely, if I may employ another metaphor, that a general and his commanding officers (or military strategic knowledge for that matter) — representing the genome — are constantly in a full command of all the military units (populations of cells, tissues, organs) and that battles are always won by the strict obedience of command alone. Battles are won also when some military units (heroes) sensitively adapt

to new unpredictable situations (environments) and/or disobey a foolish command. A wise and successful general (military strategy *sensu lato*) consequently learns to avoid foolish commands in order to win more battles, or else he loses his command (goes extinct). He, the general and his commanding officers, will resent and resist this, and rarely admit it, but in fact will tend to give more freedom to efficient units able to win the battles for him or in spite of him.

Life is even more complex than military games, and rarely has a simple rhythm of a marching unit. "Disobedience" constantly enhances variation needed for a balanced number of units and heroes, increasing the probabilities that battles are won in spite of weak or wrong commands. It is in the interest (survival) of the commanding unit (replicators) to trust the troops and to modify future commands (reverse transcription) according to the experience of the field units (epigenesis); it is also in the interest of the commanding officers (genes) to maintain a pretense of unquestionable command from above. The subtle feedbacks often punished as disobedience nevertheless exist, for a command is rarely given twice if proven wrong the first time. For that matter, the chance to give a wrong command (especially if lethal) the second time exists only if the first is disobeyed.

The liberal epigenetic variability increases the efficiency of natural selection (or processes of the nonequilibrium thermodynamics for that matter (Prigogine 1980)); the canalization of complex adaptations or developmental structures is enhanced. It cannot easily translate into the genome without destroying the genome's conservatism essential for stability. A strong barrier, crossed only in exceptions and "emergencies," must therefore exist between the two sources of variation. It may be crossed if something akin to Steele's (1979) reverse-transcribed genetic information or Waddington's (1953, 1961) assimilation is possible, which according to Campbell (1982, p. 199) it is: "... the number of genes with some capacity to inscribe into the germ line the changes induced in the soma could be substantial." It is time to admit that Goldschmidt (1940) came often close to this idea, and in spite of his infatuation with genes, brushed repeatedly on identical conclusions.

Extensive epigenetic (developmental) variation, however, is needed less for the "replicators," rightly the guardians of the status quo, than for the survival of the phenotype confronted after each reproductive cycle with new environments (Bryan and Larkin 1972; Chesson 1978; Morse 1980). The genome (i.e. my first source of variation) prepares the offspring at best for what was available with hindsight (akin to stabilizing selection); natural selection acting upon products of epigenesis (the second source) adapts the vital features and life-history traits to the present (akin to directional selection). Undoubtedly, natural selection must act on the products of both sources of variation simultaneously (Fig. 1) to ensure successful survival and reproduction (Salthe 1975). As in the case of evolution of species discussed by Alberch (1980) "... an orthodox neo-Darwinian perspective amounts to assuming an unlimited source of variation with an omnipotent selective force, and that selection *optimally* solves the functional problem in every case." However, "*morphological variation is constrained and natural selection is sloppy*" (p. 653, 654, the last emphasis mine).

Incidentally, I consider the name-giving habit unattractive and take neo-Darwinians, Modern Synthesists, Hyperdarwinians (Gould 1982b) or Epigeneticists all as a variable flock of Evolutionists. After all, each contributes to the paradigm of evolution in a unique way and in the spirit of Darwin himself who often deliberately did not complete the story-to-be for tactical, heuristic, or Victorian reasons, or because of missing evidence and sheer error in thinking. The most active defenders of his ideas and personal friends acted the same way (according to Stone 1980; Ruse 1982). Thou should not "belittle the triumphs of their forebears" and foster "... the arrogant supposition that we have better insights and greater understanding than our predecessors" (Futuyma 1978, p. 41). However, in all fairness I must voice some sympathy with the evidence and views presented by Løvtrup (1982a, e) that, more correctly, a flock of Lamarkians [however not in the sense of the discredited "Russian" interpretation (Medvedev 1969)] is actually what we are.

Darwin's main argument for natural selection was that many more young are produced than survive. Most fishes, for example, demonstrate this idea extremely well (Cohen 1977, p. 237): the number of zygotes produced exceeds by many orders of magnitude the number of offspring that survive and reproduce. It is therefore obvious that selection can operate more effectively during early ontogeny when both genetic and epigenetic variations are represented through a maximum number of individuals.

Each act of successful reproduction involves new epigenesis. The specialized multicellular organism is reduced to a nonspecialized single cell. Ontogeny must begin anew, as if "returned to the drawing board" (Dawkins 1982).

Survival of the overabundant stages of early ontogeny depends on (a) hard selection, i.e. selection through defective gametes, wrong instructions given by the genome, or ontogenetic failures caused by epigenetic variations exceeding viable limits (hence, somewhat expanded by me from what Whyte 1965; Wallace 1970 and Cohen 1977, but not Wilson 1980, called 'hard' selection) and (b) soft selection, i.e. natural selection for the most suitable combination of genes in the genome and phenotypic characters in the individual. In the following, "selection" will refer to soft selection only. We shall also ignore the principles by which selection operates (e.g. Van Valen 1976a; Jacob 1977; hypercycles of Eigen and Schuster 1979). One truism, however, must be stressed here in advance: because selection cannot operate in foresight, a creation of optimal solutions is unrealistic (Pittendrigh 1958; Jacob 1977; Skinner 1981) and rarely possible or feasible.

As documented in detail elsewhere, ontogeny proceeds in a saltatory fashion; changes in form and function are prepared at varying rates during longer intervals but become operational at accelerated rates during brief intervals called thresholds (Balon 1979a; 1980; 1981a, b; 1983a, b, c). Saltatory processes in ontogeny are, of course, more than variable developmental rates or sequences of instars as in arthropods. Structures which together form a system (tissue, organ) align their rates of development to become simultaneously functional (Carey and Noakes 1981) and initiate a new vital function — e.g. photoresponse, change of substratum, nutrition — at an accelerated rate. This "switch" is what I call a threshold, a rapid transition from one quality (steady state) of

organ−organ or organism−environment interaction to another. Physiologists may call a threshold an interval of ontogeny during which new or additional integrative actions (*sensu* Adolph 1982) enter the complex activity of the individual. Depending on the number of coinciding completions of structures and changing functions (actions), and their adaptive or developmental significance, the "strengths" of thresholds will vary, as will the preceding and following intervals of ontogeny (Balon 1983c). The theory of saltatory ontogeny, briefly recapitulated above, is essential for the understanding of both theories formulated later in this paper.

The consequences of genetically instructed and epigenetically operated heterochronies (in the sense of G. de Beer (1958, p. 34) and Berrill (1945), less Gould (1977)) increase available variations and facilitate a rapid selection of viable phenotypes adapted to present environments (Bradshaw 1965). When the consequences of heterochronies combine, they modify the amplitude and timing of thresholds. As to how heterochrony works, we may well accept Waddington's (1975, p. 9) explanation: "... it had become apparent that the 'gene-concrescence' itself undergoes processes of change; at one embryonic period a given concrescence is in a phase of 'competence' and may be switched into one or other of a small number of alternative pathways of further change — but the competence later disappears and if you've missed the bus the switch won't work."

As was said before, this is only part of the picture, but before we expand it, let me state that some consequences of the processes reflected in heterochrony were presented by Lindsey and Arnason (1981) in an elegant model called atroposic.

Heterochrony, sometimes superficially seen as a shift in the appearance of organ anlagen, acts in a complex manner, influencing an interrelated web of tissue interactions and a succession of inductions (Maderson 1975). In cells, tissues and other structures that are either adaptations to the environment at a particular saltatory step or developmental antecedents, heterochrony triggers a chain reaction of changes in cellular mechanics, which leads to the construction of new vital characters and functions through, for example, dissociation of inductive events. These mechanics are best illustrated by Løvtrup's (1974) example of the sf-cell which by using its filopodia and by developing a certain tension is able to pull colligocyte aggregates together until stopped by opposing forces. Similar examples are given by Trinkaus (1969), and Trinkaus and Erickson (1981). Goldschmidt (1940, p. 297) claimed that "A single mutational step affecting the right process at the right moment can accomplish everything, providing that it is able to set in motion the everpresent potentialities of embryonic regulation." I claim that a single epigenetic event can accomplish almost the same, providing its "force is strong enough" to eventually cause transcription into a germ line.

The earlier or later appearance of thresholds (Balon 1979a, 1980) in early ontogeny causes changes in morphology, physiology, and ethology (Balon 1983b). According to the functional significance of such shifts in thresholds, these shifts will have developmental, adaptive or evolutionary consequences. The variation skewed by epigenesis is channeled for greater efficiency of natural selection (Salthe 1975), although not "towards optimal phenotypes" (Lewontin 1979) as perceived by Stearns (1980), because such would mean equilibrial stasis (Wiley and Brooks 1982) and extinction.

Epigenetic changes in early ontogeny (Maderson 1975; Alberch 1980) may result in modifications of life-history traits or reproductive styles (Oppenheim 1981) and then form a basis for structural deviations (e.g. Sawin and Edmonds 1949) akin to something traditionally expected only of gene mutations. Similarly, Geist (1978) suggests that in mammals environmental influences are prenatally mediated by the mother and cause phenotypic deviations reflected in the entire population. Under special circumstances all such deviations may be incorporated into the replicators, for example, via reverse transcriptions and together with reshuffling of genes and other mutations may provide the main substrate for evolution (e.g. Bateson 1979, p. 153−162). Can we identify at least some such special circumstances?

Juvenilization

Perhaps a highly heterogenous genome can result in a lower epigenetic variation than a homogenous one. A homogenous genome might regain some variation via juvenilization (*sensu* paedomorphosis = shaped like a child, Garstang 1922), one of the special circumstances sought. Wake (1980) and Alberch (1980) presented elegant empirical examples of paedomorphosis.

The ontogenies of charrs[1] provide more such examples (Balon 1980). Two temperature induced phenomena illustrate the more subtle features of juvenilization. Low environmental temperatures around the arctic charr, *Salvelinus alpinus*, often result in a long-lasting ice cover, which precludes the surface filling of the swimbladder by air when the transition to exogenous feeding (emergence from redd) is imminent. Accordingly, cold-reared fish show a delayed morphological differentiation at the same ontogenic threshold (Fig. 2). This affects the skeletal calcification at later stages, irrespective of size (Fig. 3). Presumably, the cold-adapted charr compensates for the lack of access to the surface and the resultant empty swimbladder by a lighter axial skeleton at the same size and activity as the warm-reared charr. These and similar heterochronies in the early ontogeny of charrs determine the later life histories and often result in two forms which are maintained by allochronic reproductive isolation (Balon 1980; 1983a). The juvenilized form (altricial, as will be explained later) always remains less specialized, of different size, color and habits (for other examples, see Geist 1971; Hirshfield 1980).

The epigenetic response to environmental cues can be subtle as in the example above, with only life-history consequences, or very strong with evolutionary consequences, as in the example for the origin of chordates (Balon 1983b; see also Berrill 1955; Gould 1982a).

We can continue, still using charrs, to complete the

[1]The spelling differs from that (char) used in *A List of Common and Scientific Names of Fishes from the United States and Canada*, by the American Fisheries Society, and is preferred by the author. The reasons for this preference are the same as given by Johnson (1983, p. 988).

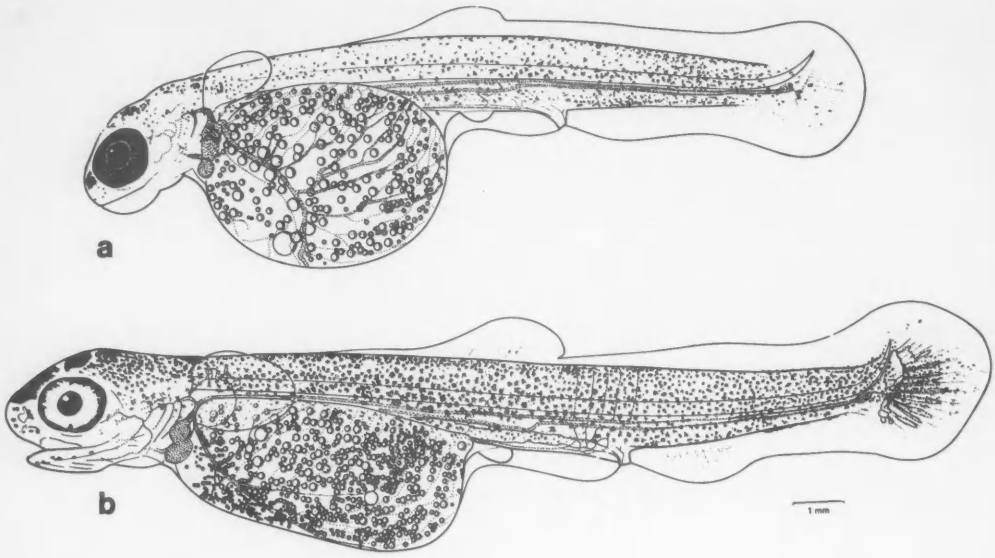

FIG. 2. State of development in (a) warm-incubated (15.9 mm TL) and (b) cold-incubated (19.8 mm TL) sunapee charr, *Salvelinus alpinus oquassa* (from Balon 1980b) showing the consequences of heterochrony.

illustration of paedomorphosis. Although fossils are scarce for Salmonidae (Behnke 1972), at least one fossil, *Smilodonichthys rastrosus* (Cavender and Miller 1972), suggests that this anadromous giant salmonid from the Pliocene was a plankton eater. Were earlier salmonids also descended from oceanic pelagic forms by virtue of their reproductive style? All the evidence regarding the evolution of reproductive guilds (Balon 1981b) is affirmative. A predecessor of the salmonids, therefore, would be a nonguarding, open substratum egg-scattering pelagic spawner (Balon 1975a) with relatively low embryonic differentiation, a long larval period, and metamorphosis preceding the juvenile period (Balon 1981c). The evolution of protective hiding of eggs and embryos may have been a consequence of invasion into fluvial systems prior to paedomorphosis. Selection would then favor higher yolk density and larger yolk size (Balon 1977, 1978), which in turn enabled earlier differentiation of structures vital for better survival after emergence. This way, the ground for paedomorphosis could have been prepared, as hiding permitted earlier appearance of many structures known to develop later in the ontogeny of nonhiding fishes. Some vital organs, characteristic of the larval period in egg-scattering fishes, develop completely during the embryonic period in salmonids and the larval period is eliminated or retained only as a vestige (Balon 1983b, c). Consequently, the life history of extant salmonids, including charrs, has most probably evolved from open substrate spawners by paedomorphosis (Balon 1980).

Obviously then, paedomorphosis is one of the saltatory switches into a new steady state in which sufficient genetic and epigenetic variations can again be maintained. In its subtle form it is a modification of ecomorphological features for a steady state less specialized than the original. In its strongest form it is an evolutionary switch to a new, more generalized homeostatic state. In both instances some of the genetic variation lost during specialization is reinstated and epigenetic variation enhanced. The phenomenon is, consequently, more widespread than generally assumed, for even the subtle cases (switch from a precocial to altricial life history) are essentially juvenilizations.

The Chen Principle

A phenotype that is perfectly adapted to its environment is rarely, if *ever*, achieved (Darlington 1977). Had this been otherwise, stable patterns or trends would be impossible. The consequences of conservative genetic variation (maintained by mutations and reverse transcriptions) are constantly controlling the excesses of liberal epigenetic variation (propelled by epigenesis) thereof preventing a fine tuned optimization and antagonizing the tendency to specialize. For overspecialization defies survival. However, if the epigenetic "insistence" towards specialization can no longer be "controlled" by the gene products, overspecialization occurs and extinction is inevitable. Under certain conditions, paedomorphosis reinstates the gene "control" and acts to insure the extension of survival. Bateson (1979, p. 22) expressed the same idea differently: "The barrier which prohibits 'Lamarckian' inheritance precisely protects the gene system from too rapid change under possibly capricious environmental demands." He also assumed that somatic changes might precede genetic changes and therefore might "partly determine the pathways of evolution . . ." (p. 160).

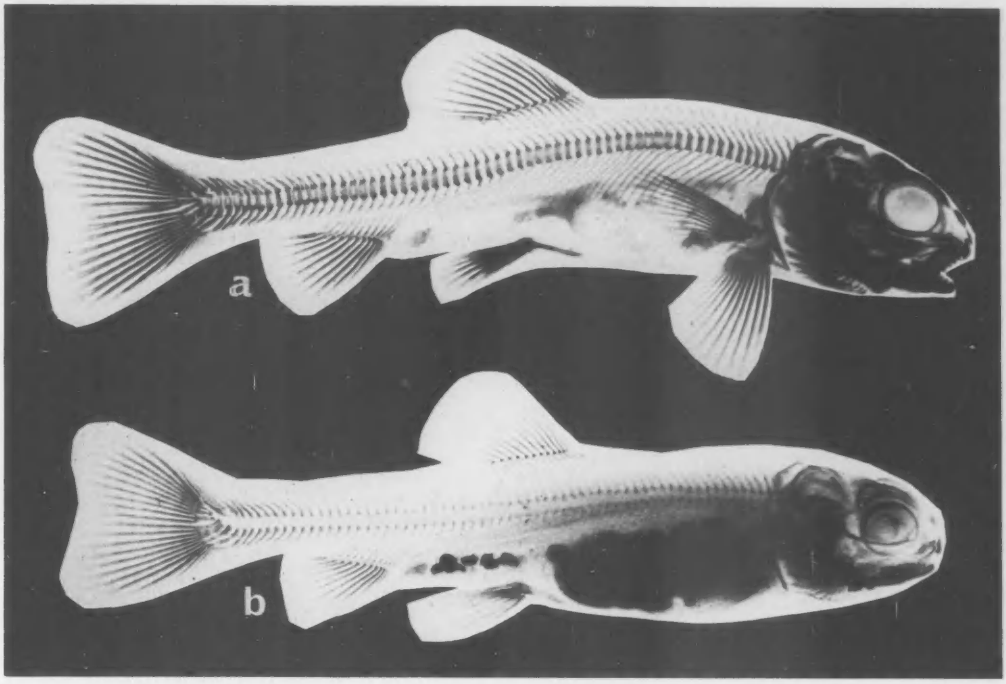

FIG. 3. Different calcification of skeletal structures in (a) warm-incubated (39 mm TL) and (b) cold-incubated (39 mm TL) sunapee charr (after Fig. 23e, g in Balon 1980b).

This section, however, was designed to end in another direction. "The bamboo bends before the wind," in a Japanese metaphor, and Bateson (1979, p. 103) precedes this with "'Stability' may be achieved either by rigidity or by continual repetition of some cycle of smaller changes, which cycle will return to a *status quo ante* after every disturbance. Nature avoids (temporarily) what looks like irreversible change by accepting ephemeral change." In other words, the steady state is maintained by variation clustered by saltatory processes, the only means to prepare for future perturbations by adaptation to past perturbations. I can hardly express this phenomenon better than Alberch (1980, Fig. 1), although on a phenotype level, one correction is inevitable. Only two epiphenotypes, not three or more clusters of variations, are necessary (although more than that are possible), because only two answers (steady states) are needed to answer any question environmental perturbations may present. (The topic of two states will be the central theme of our last section.) Therefore, Fig. 4 presents a version of Alberch's plot of canalized variation into saltatory steady states modified for entire phenotypes. Alberch perceives the epigenetic regulatory properties of this system as follows: "Small perturbations will be regulated back to the system's original domain. Large perturbations, however, may place the system into another domain of attraction where it will be pushed into a 'steady state' different from the original one" (p. 655). Our variations behave like some kind of irregular quartz crystal oscillators whose importance in a homeostatic system cannot be overemphasized (Kauffman 1969; 1974). Heretically, the proposed (e.g. Charnov 1982) Evolutionary Stable Strategy (ESS) may be only one of the patterns caused by the above process of maintaining epigenetic homeostasis.

Because of the constant interaction between the two sources of variation under "stabilizing and directional selection," each caused by an environment other than the environment selected into (e.g. lag load of Maynard Smith 1976b), an optimization of evolutionary units or trends cannot be afforded so all must alternate endlessly around a homeostatic state or, if necessary, between two steady states. Van Valen (1973) named another similar phenomenon "the Red Queen's hypothesis," after the Queen's statement to Alice: "Now *here*, you see it, it takes all the running *you* can do to keep in the same place" (Carroll 1871). Here, however, my zoologist's respect for priority overrides the infatuation with the adventures of Alice. I cannot ignore the long existence of the Chinese word "chen" in literature and its association with the meaning "to stand still" but also "to gallop at full speed" (Bloodworth 1967, p. 188). If true (see also the Chinese character "pu" which means to walk but also represents stopping and starting), then the Chinese could have been long aware of this phenomenon and contracted it into a single sound. (This amusing bissociation Bloodworth found in *The Chinese Unicorn* may be incorrect

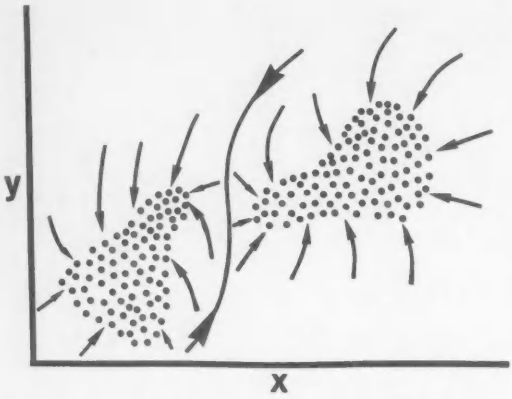

FIG. 4. Simplified diagram showing a hypothetical distribution of variation (x,y) into clusters of steady states (e.g. steps) as a consequence of saltatory homeostatic processes, divided by canalization (e.g. thresholds). Every set of environmental requirements (e.g. forces) can be accommodated by one generalized and one specialized steady state, as if only two answers (i.e. steady states) were needed to any question environmental perturbations present (based on Fig. 1 in Alberch 1980).

and caused by sloppy transcription of these sounds in the "mid-nineteenth-century Chinese–English dictionary," for I failed to find them associated in more modern dictionaries. It should equal in ideation the Red Queen's metaphor and so do for our purpose. It is also consistent with my belief that phenomena of consequence were mostly, intuitively or not, already perceived by our forebears.) Furthermore, the Red Queen's hypothesis (Van Valen 1974; 1976b) "contains a 'zero-sum' assumption, according to which an increase in fitness of any one species is exactly balanced by the sum of the losses of fitness of all the others" (Maynard Smith 1976a, p. 325). It illustrates a different phenomenon than our constant oscillation (variation) around and in support of a homeostatic system. I, therefore, propose to call the endless reestablishment of variations through reproductive cycles (via the two sources so far identified) — in order to maintain by saltatory 'forces' the steady states recognized as any evolutionary units or, in a strict sense, as steps in organism's ontogenies — the Chen Principle.[2]

The Central Theme — Biological Dichotomy

If we scrutinize the available data on life-history styles (as summarized, for example, by Stearns 1976, 1980), a pattern of two alternating traits often emerges. Populations or even demes of each species can alternate between these two traits (Berven et al. 1979). Stable and/or competitive conditions will favor steady states of specialized traits, perturbed and/or colonizing conditions will favor steady states of generalized traits. This coincides with Hennig's (1966, p. 235) paradigm that "... processes of species cleavage are the characteristic feature of evolution." Is the same biological process responsible for the omnipresence of this dichotomy?

The epigenetic processes by which an adaptation to a present environment can be rapidly achieved, as explained earlier, are reflected in heterochronies. In prolonged uniform and stable conditions specialization can become "overdone" by trapping an organism in such a narrow range of variation that any perturbation cannot be compensated for and becomes terminating. This trend can be reversed by juvenilization and thus extinction postponed or bypassed by survival of the juvenilized progeny. Beyond the time scale of generations, identical processes are probably responsible for speciation and paedomorphosis, i.e. the processes which cause changes in life-history traits and reproductive trends may be canalized into thresholds "strong" enough to switch into a new evolutionary unit.

Following the long accepted terminology for birds (e.g. Ricklefs 1979), I have used the term altricial for describing generalists and precocial[3] for describing specialists. The most general features of the two stable states are, relatively small and incompletely developed young in the altricial and relatively large and completely developed young in precocial forms (Balon 1983b). Therefore, the life-history traits and evolutionary units, as consequences of epigenetic processes, form "Altricial⇌Precocial Dynamic (nonequilibrium) States" (or APDS for short).

Naturally, my implication is not that I have formulated something completely new. Much of the above stems from others (e.g. Schaffer and Tamarin 1973; Schaffer 1974, 1979; Wilbur et al. 1974) and my own dissatisfaction with the uncritical or even inappropriate application of the *r*- and *K*-selection concept (Nursall 1974; May 1976) to life histories (Pianka 1978) and evolution (Gould 1977; Vrba 1980). There are, of course, some similarities (Noakes and Balon 1982): The altricial generalist is vaguely related to *r*-selected, progenetic, paedogenetic (Gould 1977) or hypomorphic forms (Løvtrup 1978) as is the precocial specialist to *K*-selected or neotenic (*sensu* Gould 1977) forms. The two steady states, altricial and precocial, cause the ecosystem to appear as if in two phases which, according to Maynard Smith (1976a, p. 330), would violate the Red Queen's hypothesis, i.e. "Since there is no reason to expect a zero-sum assumption to hold exactly, it is suggested that an ecosystem may be in one of two evolutionary phases: a convergent phase, with the rate of evolution decreasing, or a divergent phase, with evolution accelerating."

However, the major reason against using the *r*- and *K*-selection concept instead of altricial and precocial states is that these states reflect the epigenetic processes responsible for their formation and not life-history parameters of arbitrary or unknown origin (as in Murphy 1968; Constantz 1979; Felsenstein 1979; Luckinbill 1979; Stearns 1980; Casewell and Hastings 1980) or the state of an ecosystem. After all, even the alternative life-histories in protogynous fishes and shrimp (Gross and Charnov 1980; Charnov 1981) may be

[2]In doing this, I consider my debt for destroying the legend of the Chinese origin of domesticated carp in Europe to be paid (Balon 1974).

[3]This should not be confused with the usage of "precocious" to designate early maturation at a small size, for example, in salmon males.

such parameters only, i.e. patterns formed by the above processes. Since the terms altricial and precocial can be similarly used when referring to invertebrates, fishes, amphibians, reptiles, or birds, and are therefore of high comparative value, I prefer them to the probably synonymous paedomorphs and peramorphs proposed by Alberch et al. (1979) or dispersal and maintenance phenotypes proposed by Geist (1978).

The same sets of attributes which characterize invertebrates and lower vertebrates as altricial and precocial forms may not apply to higher vertebrates, especially placentals. The ultimate reproductive specialization — placental viviparity — enabled the evolution of the central nervous system to an unprecedented degree and caused a kind of "reversal in priorities": mental competence combined with precocial physical attributes (i.e. larger) enables now an extension of the usefulness of specialization into a "dispersal phenotype" (Geist 1978) which replaces the altricial form, whereas the "maintenance phenotype," physically less developed and mentally less competent, represents our precocial form. While a dichotomy clearly remains, the "reversal in priorities by mental competence" (RPMC) in mammals becomes a new epigenetic force which determines the observed patterns (Geist 1971). At this point some felt — in spite of infatuation with genes — that "memes" warrant introduction (Dawkins 1976). Be that as it may, the mental competence evolved as an innovation powerful enough to change earlier priorities in energy allocation and use, turning into an advantage traits of lesser survival value in forms without the mental competence.

A synthesis of the main ideas presented in this article is attempted in Fig. 5. The sequence of ontogenies (reproductive cycles, generations) reflects the epigenetic tendency for specialization; heterochronous shifts of the period boundaries (thresholds) cause different life-history traits (Balon 1983b) with altricial generalists at the beginning (left) and precocial specialists at the end (right) of the trajectory. Either generalists or specialists are possible in a constant saltatory seesawing between one or both "altricial⇌precocial dynamic states." The generalists, with a highly heterogenous genome, the broadest epigenetic variation, and an ability to survive most perturbed environments, are usually organisms of early maturation and/or long reproductive interval (dotted area), delayed somatic differentiation, and low reproductive cost. (Small size is not always an attribute of altricial form, as in charrs (Balon 1980), but large, well-developed embryos can be produced by small adults within a taxon as, for example, in darters (Paine 1983). After all, "the lion is very close to being a pussycat. Mere size seems to be irrelevant. Form is what matters" (Bateson 1979, p. 169). Nevertheless, the tendency to increase size along the specialization trajectory (Cope's Rule) is common (but see the RPMC).) Because early ontogenetic features of a highly general nature are retained by numerous offspring, a constant, extremely broad range of variation is possible. Given lack of severe environmental perturbation and increasing competitive pressure, selection will favor specialization.

If structural constraints permit, such specialization may cause the explosive formation of evolutionary units (cf. Vrba's 1980 "effect hypothesis"); for example, the trophic adaptations in cichlids in African lakes (e.g. Liem 1974; Liem and Osse 1975; McKaye 1978; Greenwood 1981; Yamaoka 1982), with the single reproductive style of mouthbrooding. Conversely, a single evolutionary unit like cyprinidontiforms, may specialize into all possible reproductive styles of nonguarders, guarders and bearers (see Seegers 1980; Parenti 1981), and remain largely feeding generalists.

After a number of ontogenies in one direction along the specialization trajectory (Fig. 5), both sources of variation may be considerably "used up." Age and size at maturation will be delayed and the high reproductive cost will be shared by a few precious zygotes. The lifespan may be prolonged, either by the senescent period, which is of no reproductive value, or to permit semelparity. This reduces variation so much that environmental perturbations which were previously accommodated, now become totally destructive (with a possible exception of RPMC). I use the term hypermorphic evolution for this trajectory of adultation.

If the only possible sequence of evolution were hypermorphic (Løvtrup 1978), every species (or evolutionary unit *sensu lato*) would become extinct much faster than experienced. However, such species reacts to unpredictable environmental perturbations by oscillating at a steady state or by switching to the other needed steady state — from altricial to precocial and back to altricial. I cannot resist declaring this as a central biological dichotomy which conforms well with the "opposites in a dualistic 'either-or' view" (Jantsch 1975).

In extreme cases of specialization, and given certain conditions that we are now unable to positively identify, these canalized forces can become strong enough to cause special thresholds called juvenilization or RPMC and again convert a precocial into an altricial with somewhat reduced variation (e.g. Bretsky and Lorenz 1970; Snyder and Bretsky 1971). Under even stronger conditions such thresholds can be canalized into paedomorphosis which prevents extinction and creates a new evolutionary sequence along the paedomorphic trajectory or affects a new morphological steady state of a higher (taxonomic) magnitude. (It might have been noticed by now that I give unequal rank to the otherwise synonymous terms, using juvenilization for life-history and paedomorphosis for evolutionary phenomena.)

Summing up, ample evidence for the omnipresence of the twin steady states — altricial and precocial — can be found in the literature (e.g. Fenderson 1964; Frost 1965; Rupp and Redmont 1966; Messieh 1976; Kobayasi 1976; Copeman and McAllister 1978; Leggett and Carscadden 1978; Constantz 1979; Bruce 1980; Balon 1980, 1983a). With respect to reproductive styles, fishes are probably the most diverse of all vertebrates, followed closely by amphibians (Salthe and Mecham 1974; McDiarmid 1978; Bogart 1981). Birds are greatly limited in reproductive styles (consider the questionable distinction of "semi-precocial," Ricklefs 1979), so are altricial marsupials and precocial placentals in mammals (Low 1978), although in the latter cases subtle APDS are, for example, reflected in relatively altricial rabbits with small naked young hidden in burrows, and precocial hares with larger furry young in nests above the ground, and RPMC exhibiting mountain sheep (Geist 1971). Many other organisms could have followed the same dichotomy (Hennig 1966; Løvtrup 1977) including man (Geist 1978; Lovejoy 1981; Stanley 1981). Neanderthal man was probably precocial and Upper Paleolithic man altricial (Geist 1981),

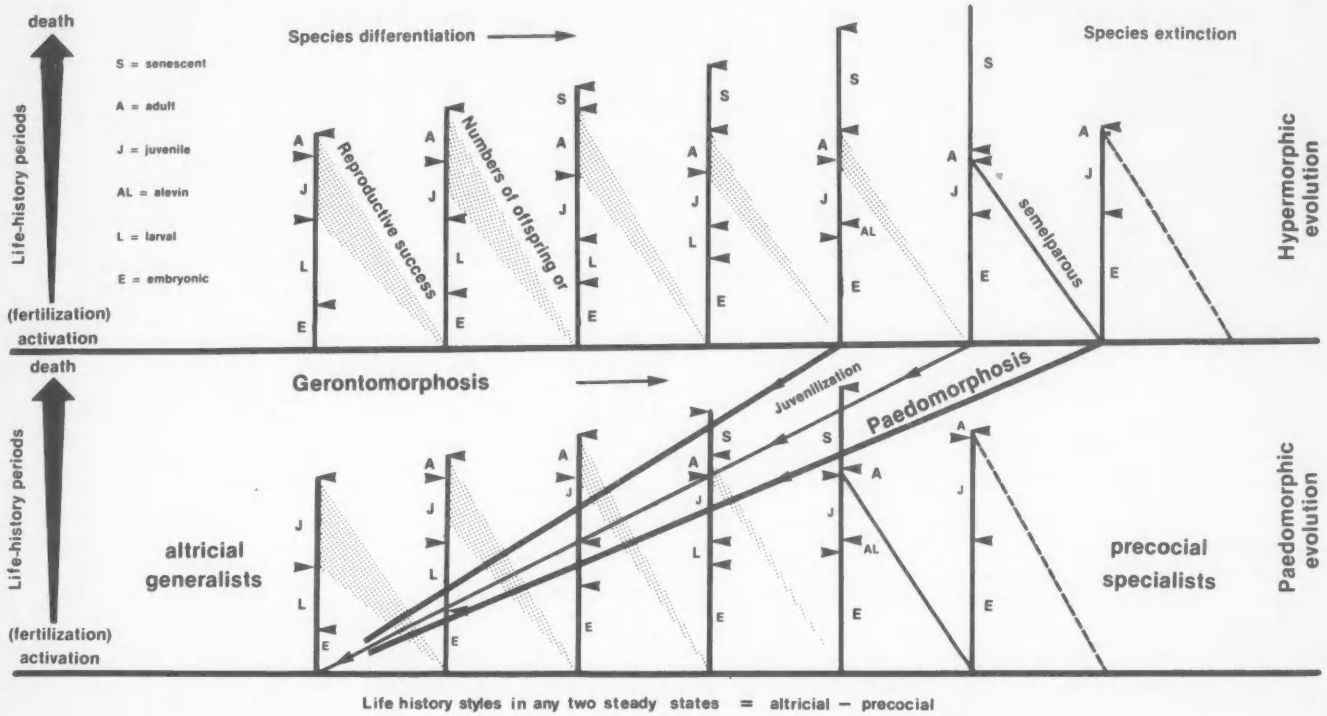

FIG. 5. Scheme illustrating possible ontogenies = life history styles (vertical lines) in a sequence of increased specialization (left to right) and, under certain conditions, despecialization by juvenilization/paedomorphosis (from upper right to lower left). The relative duration of ontogenetic periods (arrowheads = thresholds) changes during specialization from altricial generalists (left) towards precocial specialists (right), concomitantly the reproductive success = number of offspring (dotted areas) is reduced and paralleled by truncation of adult, elimination of larval and prolongation of senescent periods. Any two of the vertical ontogenies can represent, at the same time or at different times relative to the position of the specialization trajectory, the dualistic steady states named "altricial ⇄ precocial dynamic states." In both trajectories, the hypermorphic (upper) and the paedomorphic (lower) one, specialization equals gerontomorphosis.

whereas recently the bushman-like forms appear to be the most altricial people of the paedomorphic genus *Homo* (these are rather common sense predictions without a comprehensive review of literature). Is our subconscious sympathy for imaginary (Gould 1979) or real altricial brethren (van der Post 1975) motivated by our respect for better adaptation for survival?

Epilogue

Fools do rush in where angels fear to tread,
but cell biologists are no angels and I am
no fool.
N. J. BERRILL (1983)

It is only because I believe that communication of ideas, right or wrong, is most essential for progress in science, that I risked to formulate the above concepts. The "Chen Principle" formalizes the theory of constant epigenetic variation required for the maintenance of any viable steady state recognized as an ecological form or evolutionary pattern. The "Altricial⇌Precocial Dynamic States" formalize a related theorem that each such pattern may exist in two steady states as an answer to environmental requirements or vicariance events (Wiley 1981) at any given time. I believe that both theories explain reasonably well the processes we came to perceive as a result of partly closed thermodynamic systems "in terms of information and cohesion" (e.g. Wiley and Brooks 1982 and references therein) within the open-ended system of nonequilibrium thermodynamics in terms of energy (e.g. Prigogine 1980; Johnson 1981). However, I am far from satisfied with my arguments and do not believe that any of my current claims provide a definitive answer to the questions raised. Therefore, as a *verbum sapienti*, I will end much in Stern's (1982, p. 146) context, and let Carroll have the last word:

"What is the cause of lightning?"

"The cause of lightning," Alice said very decidedly, for she felt quite certain about this, "is the thunder — no, no!" she hastily corrected herself. "I meant the other way."

"It's too late to correct it," said the Red Queen: "when you've once said a thing, that fixes it, and you must take the consequences."

Acknowledgments

I thank David L. G. Noakes, Christine Flegler-Balon, Jeffrey Baylis, Richard Dawkins, David Lavigne, Susan Mahon, Michael Paine, and Joan Cunningham for many useful comments on the various drafts of this essay. Otto Ulč enthusiastically misled me into using the "chen" phenomenon but his wife Priscilla gave little Chinese support for it (except coming up with the "pu"); their contribution is much appreciated. This paper was prepared while I was supported by Natural Sciences and Engineering Research Council of Canada grants.

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Climate and Fisheries. *D. H. Cushing. Academic Press (London) Ltd. 1982. 373 p. 28£ (U.K. only) $49.50 (U.S.)*

Relationships between physical oceanography, meteorology, and trajectories of exploited marine fish populations have taken on new precision during the past dozen years. D. H. Cushing has carefully pieced together the story of many of these relationships by examining different case histories having a sufficient number of things in common to convince the skeptical ecologist that the field has been progressing.

The professional fisheries worker will find that the first two chapters are unnecessary. These chapters are an introduction for readers from other fields. They are light treatments of traditional fishery subjects such as: the industrialization of fisheries, the life histories of fishes, and how fisheries focus on life history periods of fish. The last three chapters also seem unnecessary because they are largely summaries that seem repetitious of summaries following each chapter.

The seven main chapters of the book are a masterful synthesis of the effects of long-term, physical environmental change on ocean fish populations and fisheries. Many fisheries throughout the world are reviewed. The work is heavily weighted toward northwest Europe and does not treat interesting situations that have been documented for North America. The historic descriptions of several Scandinavian herring fisheries over several centuries are fascinating. Temporal alternation of Hokkaido herring and Japanese sardine, and the similar alternation of Californian anchovies and sardines are reviewed. The twentieth-century warming of the North Atlantic is documented with case histories from the North Sea, and the cod fisheries of Iceland and Greenland. Among the North Sea changes described are those of the invertebrate plankton and benthos assemblages, as well as herring, sole, and gadoid population shifts. Changes in the Arcto-Norwegian and Baltic cod populations are well treated.

A complex of biological phenomena is dealt with along with atmospheric and hydrographic trends. Effects of changes in food availability and related changes in growth rate of fish are described. The Russell cycle of shifts in plankton and neuston in the North Sea through the mid-twentieth century is reviewed and interpreted against larger-scale physical events. Evidence for the relation between long-term changes in the time of onset of Spring productivity and subsequent increase in gadoid fish in northwestern Europe is discussed, along with likely relationships between primary production, secondary production, and fish production. Cushing relates westerly winds over the British Isles, and advection of water into the North Sea, to changes in *Calanus* and *Pseudocalanus* abundance, and subsequently to changes in the stocks of several species of exploited fish. The evidence suggests that the changes in fish stocks are a direct result of changes in food availability.

A good review of El Nino physical oceanography is presented along with a description of the productivity relationships in the upwelling system off Peru. These relationships are disrupted by El Nino. The author gives a pithy account of the biology of the anchoveta, and the relationship between anchoveta productivity and the productivity of guano birds.

Mortalities of organisms during exceptionally cold winters have been major phenomena in the North Sea. Cushing reviews winter-kill records of invertebrates and fish, and describes the meteorological circumstances in northwest Europe associated with winter-kill. He points out that strong year-classes of sole often follow winter mortality of adult sole, so that the stock shows a net increase in numbers. A few pages are devoted to a historical reconstruction of tilefish mortality off the Atlantic coast of the United States during the last century. It is postulated that the deaths were due to an interplay between cold and warm water from the Labrador current and the Gulf Stream.

The work is clearly valuable to physical oceanographers, meteorologists, and fisheries scientists. It would make a fine text for a special topics course in fishery oceanography for advanced university students.

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(R489)

Handbook of Darters. *Lawrence M. Page. TFH Publications, Inc. Ltd., Neptune City, New Jersey. 1983. 271 p., 40 figs., 308 color illus., 89 distribution maps. $29.95 (U.S.)*

Only a few groups of fishes have the devotion of a large enough corps of professional workers and of fish watchers to warrant their study being referred to as a discipline. The darters constitute one of these groups, and now the Darterologists have their handbook. Of major interest in the darters is the beautiful and sometimes bizarre colors they display, particularly at spawning time. This book will delight all those interested in the darters since it brings together in one place color illustrations of all of the 131 species currently known. The intensity with which this group is sought after is indicated by the addition to the introductory notes of three species that were newly recorded after the book had been completed: *Etheostoma baileyi, E. rafinesquei,* and *E. barrenense*.

This book, however, goes far beyond being simply a picturebook of the representatives of this interesting subfamily of the family Percidae. As stated in the introduction, it consolidates information on the systematics, morphology, distribution, and ecology of this group of small fishes native only to North America.

The taxonomic treatment alone is a considerable contribution. Since I am not a Darterologist, I called on one for interpretations of the work. One of the problems over the years was to organize the large number of closely related forms (91 in the genus *Etheostoma*) into meaningful subgenera. There will always be quibbling over subgenera, but the arrangement here is apparently far superior to that used in the past. This is probably best exemplified in Page's

definition of the subgenus *Oligocephalus*, which had been considered by many to be a "catch-all" group probably containing unrelated forms. Page has attempted a clear diagnosis of each subgenus. There are clear accounts of each genus, subgenus, and species, and the tables that summarize morphological characteristics of the various subgenera are extremely useful and accurate since they represent counts and measurements made on hundreds of specimens.

A text at present in use as a summary of the North American fauna is "The Atlas" (Lee et al. 1980). Readers using both books may wonder at the difference in number of species. Page included *Percina gymnocephalus*, which had not been described when the Atlas appeared, he separated *P. carbonaria* whereas in the Atlas it was included in *P. caprodes*. *Etheostoma meadiae* of the Atlas was included in *E. stigmaeum* by Page, and Page included two Mexican species (*E. australe*, *E. pottsi*) beyond the territory of the Atlas.

Although the information on each species is organized under the headings Description, Range, and Natural History, there are also chapters on Ecology, Morphological Evolution, and Zoogeography, which include considerable information applying to the group as a whole. There is a key to all the species treated, it is well illustrated, tested before publication, and appears easy to use.

The literature on this group is extensive. It would appear to have been thoroughly treated since it includes approximately 360 citations. Drawing the literature together in one place is a service in itself.

Unusual but useful additions are appendices that list (1) the species and the political areas in which each occurs, (2) the political areas and the number of species in each, and (3) selected publications on the freshwater fishes of each area.

An extensive index of common names, scientific names, and synonyms is provided and subspecies are conveniently indexed in reverse order as well. The index would have been easier to use if the genera were in bold type and the names within genera indented.

In fact my only disappointments in the book involved editorial details over which the author probably had no control. Most of these are only minor annoyances associated with trying to use the book. Several editorial decisions lead to the need for a lot of page flipping. The distribution maps are grouped at the end and hard to find becaue they are referred to by map number instead of page number. Similarly the color illustrations are dispersed throughout the text, are cited by plate number, and although the plates are part of the pagination they have no page numbers. The publisher is supposed to have the best of facilities for the printing of color illustrations. Unless my eyes deceive me I feel that the color alignment of many of the plates may not have done credit to the time and care taken by the photographers. I'm aware that commercial presses have to advertise to stay in business, but to me the insertion of a double page of color advertisement between numbered pages 144 and 145 was not a good design feature.

None of these small problems seriously detracts from the considerable contribution of this volume to our knowledge of this colorful and interesting group of fishes. Anyone interested in the darters or in the freshwater fishes of North America should have this book handy.

LEE, D. S., C. R. GILBERT, C. H. HOCUTT, R. E. JENKINS, D. E. MCALLISTER, AND J. R. STAUFFER. 1980. Atlas of North American freshwater fishes. North Carolina Biological Survey, Publication 1980-12: 854 p.

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(R498)

Books received/Livres reçus

July/juillet 1983

Freshwater Wilderness: Yellowstone Fishes and Their World. *John D. Varley and Paul Schullery. Illustrations by Michael Simon. Yellowstone Library and Museum Association, Yellowstone National Park, Wyoming 82190. 1983. 132 p. $19.95 (U.S.) hardbound; $12.95 paperbound.* This book is a comprehensive survey of more than twenty years of scientific study. It treats management, fish behavior, population dynamics, and other natural history topics. It will be of interest to the general public as well as managers. [R513]

Collins Guide to the Sea Fishes of New Zealand. *Tony Ayling. (text and line drawings). Color paintings (48) by Geoffrey J. Cox. Collins, Auckland, Sydney, London. 1982. 343 p. $19.95 (U.S.)* The book presents the entire fish fauna of a 4.5 million km^2 rectangle of ocean around New Zealand. Its primary concern is identification of fishes although additional information on biology, ecology, and behavior are included. The fish are ordered according to taxonomic groupings. [R514]

A Guide to the Australian Penaeid Prawns. *D. L. Grey, W. Dall, and A. Baker. Department of Primary Production of the Northern Territory, Darwin, Australia. 1983. 140 p. $12.95(A) plus postal and packing charges outside Australia ($2.00(A), surface mail; $6.00(A), air mail).* This book provides an overall taxonomic guide to commercial and semi-commercial Penaeid prawns in Australian waters. It will be useful to industry, scientists, and amateurs. Clearly labeled line drawings, a glossary of terms, and explanations on how to use the keys are included. [R515]

Theory and Management of Tropical Fisheries. *Edited by D. Pauly and G. I. Murphy. ICLARM Conference Proceedings 9. International Center of Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organization, Cronulla, Australia. 1982. 306 p. $17.50, softbound; $21.50, hardbound via surface mail ($11.00 extra for airmail).* These workshop proceedings represent the current state of the art so it is not surprising the participants failed to reach a consensus on several important matters. The workshop was held 12–21 January 1981 in Australia to help answer questions regarding the continual but rational exploitation of the tropical fish resources. [R516]

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Announcements/Avis
Editorial — **J. M. Reinhart**

Articles

Bacteria decomposing amino acids in bulk-stored capelin (*Mallotus villosus*) — **J. Kjosbakken, I. Storrø, and H. Larsen**
Optimal fisheries investment: comparative dynamics for a deterministic seasonal fishery — **A. T. Charles**
Optimal fisheries investment under uncertainty — **A. T. Charles**
Influence of deteriorating water quality on growth and development of chum salmon (*Oncorhynchus keta*) larvae in a Japanese-style keeper channel — **R. A. Bams and C. N. H. Lam**
Stress response and blood characteristics of channel catfish (*Ictalurus punctatus*) after anesthesia with etomidate — **C. Limsuwan, T. Limsuwan, J. M. Grizzle, and J. A. Plumb**
Simulation and application of stock composition estimates — **R. C. Cook**
Acute effects of toxaphene and its sediment-degraded products on estuarine fish — **H. W. Harder, T. V. Carter, and T. F. Bidleman**
Sexual maturity, fecundity, spawning, and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada — **J. C. Mason, R. J. Beamish, and G. A. McFarlane**
A recurrent red tide in a British Columbia coastal lagoon — **M. G. Robinson and L. N. Brown**
Similarities in avoidance temperatures of freshwater fishes — **D. Mathur, R. M. Schutsky, E. J. Purdy Jr., and C. A. Silver**
A new approach to estimating populations by the removal method — **J. Schnute**
A stochastic age-structured model of striped bass (*Morone saxatilis*) in the Potomac River — **J. E. Cohen, S. W. Christensen, and C. P. Goodyear**

Notes

Counterimmunoelectrophoresis for identification of infectious pancreatic necrosis virus after isolation in cell culture — **S. Dea and M. A. S. Y. Elazhary**
Seasonal variation in weight-specific growth rates, feeding rates, and growth efficiencies in *Microgadus tomcod* — **I. M. Salinas and I. A. McLaren**
Estimation of disease incidence in fish populations — **D. D. Worlund and G. Taylor**
A time series approach to forecasting angling activity at a recreational site based on past successes — **D. N. Steinnes and R. L. Raab**
Behavior and distribution of larval and early juvenile *Homarus americanus* — **J. S. Cobb, T. Gulbransen, B. F. Phillips, D. Wang, and M. Syslo**

The English–Wabigoon River System

The English–Wabigoon River system: I. A synthesis of recent research with a view towards mercury amelioration — **J. W. M. Rudd, M. A. Turner, A. Furutani, A. L. Swick, and B. E. Townsend**
The English–Wabigoon River system: II. Suppression of mercury and selenium bioaccumulation by suspended and bottom sediments — **J. W. M. Rudd and M. A. Turner**
The English–Wabigoon River system: III. Selenium in lake enclosures: its geochemistry, bioaccumulation, and ability to reduce mercury bioaccumulation — **M. A. Turner and J. W. M. Rudd**
The English–Wabigoon River system: IV. Interaction between mercury and selenium accumulated from waterborne and dietary sources by northern pike (*Esox lucius*) — **M. A. Turner and A. L. Swick**
The English–Wabigoon River system: V. Mercury and selenium bioaccumulation as a function of aquatic primary productivity — **J. W. M. Rudd and M. A. Turner**

Letters and comments/Lettres et commentaires

Comment on evidence of acidification on some Nova Scotia rivers and its impact on Atlantic salmon, *Salmo salar* **J. Kerekes and T. Pollock**
Reply **W. D. Watt, C. D. Scott, and W. J. White**

Book reviews/Comptes rendus

Acid rain/fisheries: proceedings of an international symposium on acid rain and fishery impacts on northeastern North America **K. M. Mills**
Textbook of fish health **R. A. Sonstegard**
Strait of Georgia chinook and coho fishery. Can. Bull. Fish. Aquat. Sci. 211 **B. A. Henderson**
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Perspectives

Epigenetic mechanisms: reflections on evolutionary processes — **E. K. Balon** — 2045–2058

Book reviews/Comptes rendus

Climate and fisheries (D. H. Cushing) — **A. V. Tyler** — 2059
Handbook of darters (L. M. Page) — **E. J. Crossman** — 2059–2060

Books received/Livres reçus — 2061
Coming next month/À paraître le mois prochain — 2062–2063

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

CJFSDX40(11) 1853–2063 (1983)
ISSN 0706-652X

Volume 40, No. 11, November 1983 Volume 40, n° 11, novembre 1983

Articles

Nitrogen fixation and phosphorus turnover in a hypertrophic prairie lake
B. G. Brownlee and T. P. Murray 1853–1860

Electrophoretic identification of *Sebastes* and *Helicolenus* in the northwestern Atlantic
J. M. McGlade, M. C. Annand, and T. J. Kenchington 1861–1870

Estimating population size from relative abundance data measured with error
J. S. Collie and M. P. Sissenwine 1871–1879

Influence of hatchery smolt releases on adult salmon production and its variability
B. A. McCarl and R. B. Rettig 1880–1886

Periphyton biomass and species composition in a coastal rainforest stream in British Columbia: effects of environmental changes caused by logging
K. S. Shortreed and J. G. Stockner 1887–1895

Hydrologic control of lake susceptibility to acidification
J. M. Eilers, G. E. Glass, K. E. Webster, and J. A. Rogalla 1896–1904

Decline of *Mysis relicta* during the acidification of Lake 223
R. W. Nero and D. W. Schindler 1905–1911

Zooplankton community structure in the North Sea and Northeast Atlantic: development and test of a biological model **J. A. Koslow** 1912–1924

Population and trophic dynamics of Pacific hake (*Merluccius productus*)
R. C. Francis 1925–1943

Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods
H. L. Pratt Jr. and J. G. Casey 1944–1957

Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes **A. Campbell and D. G. Robinson** 1958–1967

Mysid life history and seasonal variation in predation pressure on zooplankton
P. A. Murtaugh 1968–1974

Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behavior investigated by a subtidal multifactorial experiment
B. B. Bernstein, S. C. Schroeter, and K. H. Mann 1975–1986

Contaminant accumulation and physiological response in rainbow trout (*Salmo gairdneri*) reared on naturally contaminated diets
J. W. Hilton, P. V. Hodson, H. E. Braun, J. L. Leatherland, and S. J. Slinger 1987–1994

Geothermal effects on stream benthos: separate influences of thermal and chemical components on periphyton and macroinvertebrates **G. A. Lamberti and V. H. Resh** 1995–2009

Effect of somatic growth and reproduction on biomass transfer up pelagic food webs as calculated from particle-size-conversion efficiency **U. Borgmann** 2010–2018

Sexual dimorphism in the adipose fin of Pacific salmon (*Oncorhynchus*)
T. D. Beacham and C. B. Murray 2019–2024

Notes

Downstream and lateral transport of nymphs of two mayfly species (Ephemeroptera)
J. J. H. Ciborowski 2025–2029

Use of the size–frequency (Hynes) method to estimate annual production of a stream fish population **G. C. Garman and T. F. Waters** 2030–2034

(*continued inside back*)

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